Plant Biodiversity Science, Discovery, and Conservation: Case Studies from Australasia and the Pacific

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Thesis by publication submitted for the degree of
Doctor of Philosophy in Ecology and Evolutionary Biology
July 2011

ABSTRACT

This thesis advances plant biodiversity knowledge in three separate bioregions, Micronesia, the Queensland Wet Tropics, and South Australia. A systematic treatment of the endemic flora of Micronesia is presented for the first time thus advancing alpha taxonomy for the Micronesia-Polynesia biodiversity hotspot region. The recognized species boundaries are used in combination with all known botanical collections as a basis for assessing the degree of threat for the endemic plants of the Palau archipelago located at the western most edge of Micronesia's Caroline Islands. A preliminary assessment is conducted utilizing the IUCN red list Criteria followed by a new proposed alternative methodology that enables a degree of threat to be established utilizing existing data. Historical records and archaeological evidence are reviewed to establish the minimum extent of deforestation on the islands of Palau since the arrival of humans. This enabled a quantification of population declines of the majority of plants endemic to the archipelago.

In the state of South Australia, the importance of establishing concepts of endemism is emphasized even further. A thorough scientific assessment is presented on the state's proposed biological corridor reserve network. The report highlights the exclusion from the reserve system of one of the state's most important hotspots of plant endemism that is highly threatened from habitat fragmentation and promotes the use of biodiversity indices to guide conservation priorities in setting up reserve networks.

In the Queensland Wet Tropics the thesis achieves two additional outcomes. A localized pilot study test the accuracy of plant DNA barcodes to estimate species richness. Species richness estimations were performed with high accuracy suggesting the suitability of the approach in poorly known floras where the identity of samples is known or from samples in a cryptic life stage that are difficult to identify. The methodology is promising for areas of the world, such as the tropics, that contain a high percentage of undescribed or poorly known taxa.

In addition, a large dataset from northeast Queensland was utilized to assess broad scale patterns of phylogenetic diversity. A linear relationship between phylogenetic diversity and genus richness is found to have high statistical support suggesting that taxon richness is an accurate predictor of hot spots of evolutionary history. When the affects of taxon richness are removed through linear regression however, a strong biogeographic pattern is unveiled. Sites with higher phylogenetic diversity than expected based on genus richness are best explained by having a lower percent of Gondwanan or endemic Australian elements of the flora. These sites have a higher percentage of Indomalayan or other foreign lineages that dispersed to Australia and are more frequent in the lowland rainforest areas below 200 meters. Phylogenetic diversity is shown to be effective at unraveling broad scale patterns of evolutionary history at the biome scale, which may prove useful for justifying the preservation of not just species but assemblages of species that represent different epochs of the earth's evolutionary history.

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Costion, C., J. Liston, A. H. Kitalong, A. Ida, and A. J. Lowe. 2011. Using the ancient past for establishing current threat in poorly inventoried regions. ***Biological Conservation* 147 (2012): 153-162**

Costion, C., D. and Lorence, 2011. The endemic plants of Micronesia: A geographical checklist and commentary. ***Micronesica* 42(1): 51-100, 2012**

Costion, C., A. Ford, H. Cross, D. Crayn, M. Harrington, A. Lowe. 2011. Plant DNA barcodes can accurately estimate species richness in poorly known floras. ***PLoS ONE* 6(11): e26841. doi:10.1371/journal.pone.0026841, 2011**

Costion, C. J. Foulkes, P. Lang, R. Brandle, and A. Lowe. 2011. Linking park boundaries is not enough – A scientific assessment of the NatureLinks East meets west corridor strategy. ***Draft manuscript***

Craig, C., W. Edwards, A. Ford, D. Metcalfe, M. Harrington, H. Cross, J. Richardson, D. Crayn, A. Lowe. Complex origins: Biome assembly and phylogenetic diversity in the Queensland Wet Tropics flora. ***Draft manuscript.***

INTRODUCTION

The Biodiversity Problem

The current loss of biodiversity has become of increasing concern today, and although it is a highly cited topic in all fields of biology, methods of curtailing the current trend and its consequences remain controversial. This is largely due to a fundamental lack of base-line data in the most bio-diverse areas of the world (Myers 1988, Baillie et al 2004). Underlying this problem lays an even more fundamental issue: how to measure biodiversity. The idea of the species as being a fundamental measure of biodiversity continues to lose its robustness with the rapid development of molecular techniques in the past two decades. Today, measuring genetic distinctness within and between species has become a routine procedure in addition to comparing species based on morphological concepts. The concept of what a species has always been debatable, but we now have biological species and phylogenetic species (Martin 1996; Jeffries 1997). Adding to this, the slow progress of species discovery and taxonomic revision results in a constant flux of accepted names for the organisms that which we study. Thus the biodiversity crisis is a two-fold predicament. The race to prevent further species extinctions is constantly beheaded by the race to understand them. The two are inextricably linked. We cannot conserve effectively that which we do not understand.

To counter this fundamental problem biologists round the world have devised different methods to establishing prioritization methods that will maximize the amount of estimated biological diversity conserved with any given socio-political initiative. Although this is a logical strategy, the question of how to best prioritize is constantly bedeviled by the fundamental problems outlined above. This review will explore the current biodiversity problem, and summarize different approaches to addressing it including traditional models, their strengths and weaknesses, as well as recent methods that have improved our capacity to meet the same end goal and aim of all conservation biologists, biodiversity conservation.

The Current Crisis

There are very few places on earth that have not been significantly altered by man. Extinctions have been documented as a result of both early human civilizations as well as modern (Pimm et al 1995; Baillie et al. 2004; Ricketts et al 2005). It has been stated that human pressures represent the greatest challenge that tropical forests have seen since the KT event when a large meteor impact disrupted the world climate and important plant-insect interactions for the next several million years (Moritz et al 2005). Species most prone to extinction are rare and localized rendering the dominant global patterns of extinction concentrated in specific areas of the globe that are rich in biodiversity and endemism (Pimm et al 1995; Baillie et al 2004). Habitat loss in these “hot spot” regions lead to immediate extinctions unlike “cold spot” regions, such as the eastern US, where after the initial colonization of Europeans, a 95% reduction of intact forest habitat only rendered four species going extinct (Pimm et al 1995).

Many varying figures and percentages have been proposed on the rate at which current extinctions exceed that of the rate of normal background extinctions before the proliferation of humans. However, although there is some debate over the exact number, there is virtually no debate over the fact that the current rate of extinction exceeds that of normal background rates by several orders of magnitude and if it continues on its current trajectory will result in the earth’s sixth mass extinction. Life on earth has survived five major mass extinctions. By studying the fossil record, scientists have been able to estimate the percentage of species lost for each of these events. In the Late Ordovician mass extinction 84-85% of earth’s species were lost, in the Late Devonian 79-83%, the End Permian 95%, the End Triassic 79-80%, and at the K/T event 70-76% of the earth’s species went extinct (Jeffries 1997).

This has led some to suggest that the current extinction crisis is comparable to natural events. Nee and May (1997) suggested that approximately 80% of underlying tree of life can survive the current extinction crisis even if approximately 95% of species are lost. The calculations used to generate this theory assumed a “field of bullets” scenario, where extinctions were chosen randomly. This data was used to support the proposal that algorithms that maximize the amount of evolutionary history preserved are not much better than choosing survivors at random. This paper however received a sharp response. Purvis et al (2000) argued that the current extinction risk posed by humans is not phylogenetically random and that calculations based on actual recorded extinctions results in the loss of significantly more phylogenetic branch length and more higher taxa than predicted by random extinction, “field of bullets,” scenarios. They brought their argument to an alarming conclusion by stating that the added loss of evolutionary history incurred through nonrandom extinction in mammals alone would roughly equate to loss of an entire monotypic phylum.

Others highlight the fact that the current extinction crisis is entirely unique in that never before has the earth been dissected by wide expanses of unnatural landscapes. Many habitats are literally landlocked by surrounding human settlements leaving resident species with severe challenges as climate change forces migration of their natural ranges. Habitat loss may be the most significant threat to biodiversity however intact habitats are still faced with others, notably over-harvesting, invasive species, pollution, and climate change. Setting up reserves for the protection of biodiversity amidst these ever present increasing threats is a complicated business.

In 2003, the World’s Park Congress announced that the global network of protected areas now covers 11.5% of the planet’s surface, which surpasses the 10% proposed target set a decade earlier. Several people however have pointed out that although this was politically expedient, the scientific basis and conservation value of the targets set have been questioned. To demonstrate this further Rodrigues et al (2004) conducted the first global gap analysis assessing the effectiveness of protected areas across the world in representing species diversity. The current global network was shown to be far from complete in representing the earth’s biodiversity. Furthermore the inadequacy of the one size fits all localities approach to conservation targets was highlighted emphasizing that many reserves are biased towards particular ecosystems and that global strategies calling for 10% of each country to be set aside in reserves are inherently flawed. Since biodiversity is skewed across the plant, protected areas should also be skewed.

It would seem the solution is simple, to establish more reserves in “hotspot” regions. The problem of effectively establishing functioning reserves in global biodiversity hotspots however could not be illustrated better by the current situation in Indonesia, in the heart of Southeast Asia (MacKinnon 2005). Southeast Asia has the highest rate of forest destruction and logging (Laurance 1999) of the world’s three major tropical forest regions. Between 1985 and 1997, 18 million hectares of tropical forest were lost to deforestation (World Bank 2001, Holmes 2002). The greatest irony in this situation is that the major cause of this was a conservation effort in China. Devastating floods in China in the late 1990’s led to a moratorium on logging in their upper watersheds. The result has not been a reduction in consumption or more sustainable harvest of their own resources but a significant increase of timber imports from Southeast Asia. The increase in demand from imports has been so great that each year Indonesia has exceeded its legal limit of harvest and has resulted in massive illegal logging networks to meet the increasing demands. These networks have been described as literally seizing control of Indonesia’s lowland forests (McCarthy 1999) by becoming a “de facto” institutional arrangement (MacKinnon 2005). Corruption is rampant, with civilian and military officials involved in harvesting and marketing illegal timber. Legal companies buy illegal timber to exceed their legal annual allowable cut. Logging occurs within National Parks yet the entrepreneurs and state bureaucrats that enable it to happen remain immune from prosecution (EIA/Telapak 2000; Jepson et al. 2001). Conflicting laws and failures in enforcement, allow both legal and illegal loggers to cut without hindrance. In 1998, over half, 32 million of 58 million cubic meters, of Indonesia’s timber supply came from illegal production (Brown 1999).

These facts alarmingly illustrate that conservation legislation in one country may lead to environmental devastation in another. The affects of globalization are now increasingly apparent and if they are not integrated into national conservation policies, these policies will be doomed to failure. It is imperative that northern industrial countries consider the majority of biodiversity that is represented in the tropics and how their actions affect this diversity. Tropical forest species are exceptionally prone to extinction. Lowland tropical forests, which contain the greatest richness of plants and animals, are currently under the greatest threat. In Southeast Asia, the Philippines, Thailand, Vietnam, Sumatra, and Borneo, all have less than 10% of their original extent of lowland forest (MacKinnon 2005).

The well established but now debatable theory of island biogeography states that a 90% reduction of habitat will result in an immediate or gradual loss of about half of the species found in an area (MacArthur and Wilson 1967, Wilson 1992). Species loss then increases through secondary extinctions. The relationships between animals and plants and their role in forest dynamics are complex and poorly understood, especially in the tropics where the majority of species are undescribed or only known from a few collections. The loss of key species in any ecosystem has far reaching effects that may go unnoticed.

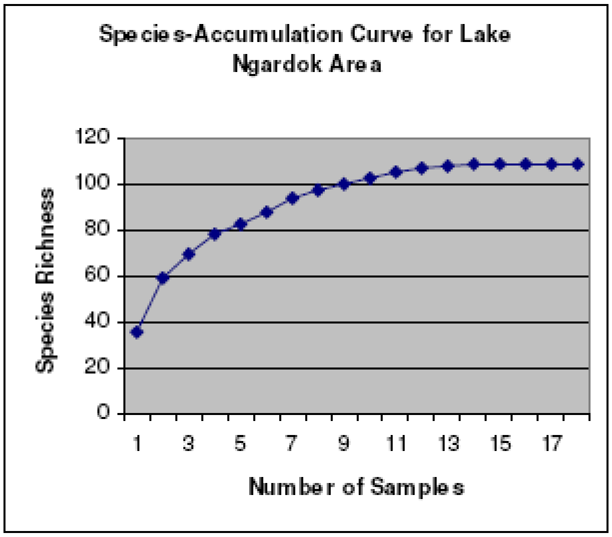
It is evident that there is a current biodiversity crisis and that a highly coordinated effort and plan is needed to alleviate its effects. Setting up reserves form a foundation of the solution, however prior to doing this it is imperative that rigorous methods are applied to ensure the areas that are set aside will have the highest biodiversity value. As once they are established it may be hard or impossible to redraw the boundaries. It has been made evident that having parks alone is not enough to curtail extinctions and habitat loss. However, establishing methods of prioritization at both the local scale where the parks are established to ensure the most important areas are conserved and the global scale giving regions global priority for protection and funding to help mitigate additional threats that are hard to legislate nationally is clearly a fundamental key to biodiversity conservation. Thus the solution to the biodiversity crisis is both an issue of measurement and prioritization.

Solutions

A commonly utilized first step approach in establishing conservation priorities for biodiversity as a whole is measuring alpha diversity. Alpha diversity measures richness of taxa at a specified locality. This straightforward approach allows one to identify hotspots of particular units of measure. One can measure for richness of species, genera, endemic species, native species, or exotic species. This is relatively simple to calculate given the area being measured is well known or comprised of species that are fully described. How then are poorly known areas measured? For example, it has been estimated (Geesink 1990; Roos 2003) that 75% of the flora in Southeast Asia is yet to be formally treated in the Flora Malesiana.

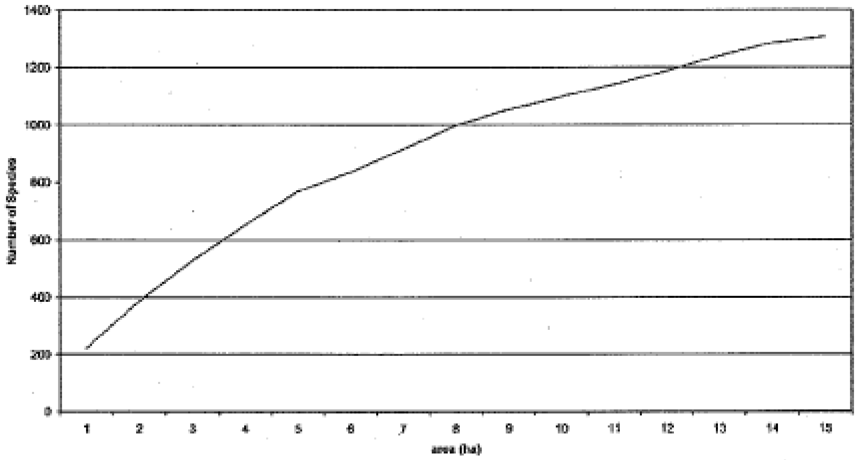
A commonly employed measure of how complete a survey of a particular area is the species area curve. Plotting species accumulation curves can give an assessment of how complete a survey has been as well as the rate at which new species are likely to be found (Magurran, 2004). This is important because sampling intensity can bias alpha diversity results. Areas that have been more intensively surveyed may falsely appear to have higher diversity than poorly studied areas. To generate a species accumulation curve the number of new species encountered is recorded in plots of the same size so that the sum total of plots represents an increasingly larger area. Typically the number of new species encountered will decrease with an increase in the number of observations until the curve flattens out. At that point it can be assumed theoretically that the survey of that area has been complete, since no more new species are being observed. Figure one provides an example of this trend. In this case it can safely be assumed that the survey is relatively complete.

Figure 1: Species accumulation curve showing a complete survey (Costion 2007).



If on the other hand the curve does not flatten out, then it is likely that there are species yet to be recorded in that area. Wilkie et al (2004) demonstrated an exceptional case of this in Borneo. After surveying 15 one-hectare plots in lowland rainforest, their species accumulation curve did not reach an asymptote. Instead it continued to climb upwards indicating not only exceptional richness in the area of study but exceptional diversity yet to be recorded (See Figure 2). This type of analysis in combination with consideration of taxonomic groups treated and yet to be treated for the flora of a region provides a basic framework for estimating species richness in poorly known areas such as Southeast Asia.

Figure 2: Species area curve for 15 hectares of tropical lowland forest from Borneo (From Wilkie et al 2004)



Perhaps the most commonly cited global alpha biodiversity analyses relevant to establishing conservation priorities are Myers (1988, 1990) and Myers et al. (2000) global biodiversity hotspot papers. The hotspot areas were identified by identifying areas that have exceptional estimated rates of plant endemism and that are experiencing massive habitat loss. Other similar approaches and analysis' include the Megadiversity Countries Strategy (Mittermeier 1988) and Mittermeier et al (1998, 1999). The areas selected are universally accepted as centres of plant diversity (Davis et al. 1994-1997). The "silver bullet" strategy proposed by Myers et al (2000) suggests that by prioritizing conservation effort in these global hotspots of plant endemism, as much of 44% of vascular plant species and 35% of all species in four vertebrate groups can be conserved in only 1.4% of the earth's terrestrial surface. Interestingly recent studies are showing support for this strategy from other taxonomic groups. Sechrest et al (2002) showed that a nearly identical hotspot distribution occurred for carnivores and primates indicating a strong correlation between plant diversity and diversity in other taxonomic groups. This suggests that the global hotspot approach may be a very effective strategy.

Identifying regions of the world where biodiversity is skewed however is only a very crude step in progress towards conservation. Reserves or networks of parks need to be selected and established in specific localities within these areas. Since funding for conservation is limited, specific areas may have to be prioritized over others. This has been referred to as the “Agony of Choice” (Vane-Wright et al 1991) or the “Noah’s Ark Problem” (Weitzman 1998) referring to the difficulty in deciding one area over another or one group of taxa over another. Clearly alpha diversity is not an effective method of addressing this question. If two areas have the same alpha diversity value and only one can be protected, how do you decide?

One method of addressing this question is an adapted form of measuring beta diversity (β diversity). Beta diversity measures the rate at which species assemblages change over geographical distance. It can show how different or similar, the floras of nearby areas are. Whittaker’s method is often regarded as the simplest and most effective method (Magurran, 2004 & Hijmans et al 2005).

The equation is as follows:

$$\beta = (S/\alpha) - 1$$

Where:

S = the total number of species over the grid cells considered
α = the average number of species in the grid cells considered

Complementarity is an adapted form of measuring beta diversity. Its aim is to capture the highest amount of diversity in as few areas or in the smallest area as possible. This enables conservationists to select the most important areas to preserve that will include the most complete representation of an area’s or a specific taxonomic group’s biodiversity. Two sites that are complementary have high turnover or beta diversity. The higher the complementarity between two sites, the higher the beta diversity or turnover there is (Magurran, 2004).

The way complementarity works is by first selecting the area with the highest species richness. The following areas are selected by having the greatest number of species not present in the previous cell or cells thereby maximizing the amount of diversity represented in the smallest amount of space. Ackery and Vane-Wright (1984) were among the first to demonstrate how powerful this technique is. They did a complementarity analysis to find the minimal set of reserves required to preserve the totality of milkweed butterfly diversity, some 158 species. Sulawesi was the first region selected with 33 species, indicating it to be the world centre of milkweed butterfly diversity. A total of 31 reserves around the world were considered required to preserve the entire taxonomic group. This method can also be applied at a more local scale where for example, a set of reserves or protected area network is being established in a particular bioregion. This technique is highly efficient at identifying the most important areas to include in the reserve network to maximize the amount of diversity represented in the smallest area (Hall 2005, Costion 2007).

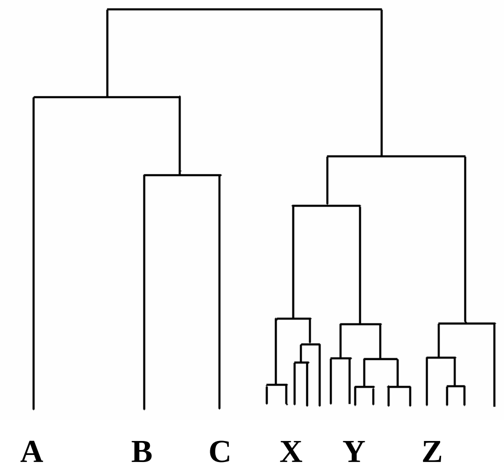
“The Agony of Choice”

Not all diverse areas are as data deficient as Southeast Asian and the Pacific. Some well-known biodiversity hotspots include the Cape Flora of South Africa, the California Floristic Province, and the Queensland Wet Tropics. In areas such as these, traditional alpha and beta biodiversity assessment methods can assist in making conservation priorities. Recently however, the use of these methods alone has been called into question. What if two areas have the same rate of endemism or taxon richness but only one can be included in the reserve network? What then would be the primary factor or factors that would enable one to be prioritized over the other? This question has received much discussion and debate and will be reviewed in this section.

The first matter to address prior to answering the question is the gap between the science underpinning the priorities being made and the methods that are actually being used today. The two obviously differ significantly. To answer the latter, we need not look hard or even into the conservation literature. Iconic animals take the stage in the public eye. Everyone wants to save the panda and the tiger, whereas countless less charismatic mammals that are just as endangered, or in some cases more so, receive little attention and support from the public. Then there are the species that don't have sentimental value to us but have some other use such as timber or medicine. These species obviously get prioritized first as well. Clearly anthropogenic factors weigh heavily on most decisions (Erwin 1991, Morowitz 1991) especially when there are political or economic incentives behind them. If one area will cost less to preserve or if preserving one of the two areas will put you in favor with potential voters, the decision is easy. These realities have caused some to raise the question whether conservation strategy should be scientifically or culturally based (Erwin 1991).

Erwin (1991) answered this question well by stating that scientific rationale will likely transcend cultural changes through time, but economic and political grounds will certainly not. By what scientific grounds then do we do this? Evolutionary distinctiveness is the answer for the overwhelming majority. Even an uncharismatic small mammal that looks like a rat that can be said to be an ancient relict or an exceptional lineage of evolutionary history will instantly transcend its lack of glamour. However, how to measure this has been another source of debate until relatively recently.

Figure 4



Whether to save the cradle or the museum of diversity has been the centre of an interesting debate. Some have contended (Erwin 1991) that recently radiated lineages, such as X, Y, and Z in Figure 4, represent the "evolutionary front" where evolution is dynamic, happening now, and most likely to take place in the future. These lineages should be prioritized for conservation to preserve the best evolutionary potential for the future. This “save the cradle” position was in direct opposition to the more conventional position that placed priority on rare endemic or relic lineages, such as A, B, and C in Figure 3 (Mittermeier 1988, May 1990).

The cradle proponents went as far to say that preserving the “A, B, and C” lineages was like preserving living fossils that were doomed to extinction. They were only of human interest and had little evolutionary value or potential for the future. Although this point of view was right to place emphasis on evolutionary potential for the future, it was flawed in its science by neglecting evolutionary potential. Recent molecular studies have demonstrated that ancient lineages such as cycads and Gondwanan conifer lineages have recently radiated after dispersal into the Pacific (Keppel et al 2008a,b). This suggests that “living fossils” are not doomed to extinction. Ancient lineages are still capable and do evolve into new species given new opportunities to do so. It also seems to support the concept of punctuated equilibrium proposed by Niles Eldredge and Stephen Jay Gould which proposed that evolutionary history or species can take million year breaks before giving rise to new species (Kerr 1997).

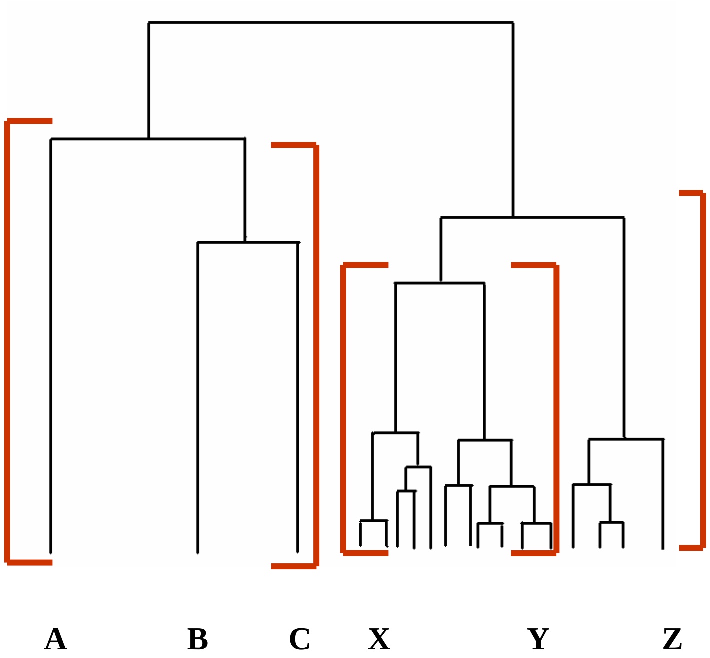
The other extreme however hasn’t proved to be most effective at maximizing evolutionary potential either. How then, is this calculated? May (1990) documented concisely how the beginnings of the “calculus of biodiversity” emerged from this argument. Clearly he argued that, the tuatara couldn’t be given equal value to that of any common and widespread skink or gecko. Its distinctness must be given weight or priority in conservation schemes. How to measure this objectively was the problem. At the other extreme Vane-Wright et al. (1990) proposed that the taxonomy of the group should be expressed as a hierarchical tree and then equal weight should be given to each sister group. This however would mean that the two extant tuatara species would weigh equally with the total of all 6,000 species of snakes, lizards, and amphisbaenas. May (1990) continued to critique another of Vane-Wright’s methods that involved counting the number of nodes between the tips and roots of a phylogeny and suggested instead to calculate the sum of all the branches at root nodes, and thus the beginning of Phylogenetic Diversity theory or the “calculus of biodiversity” emerged.

May further suggested the optimal approach would run a complementarity analysis weighted by taxonomic distinctiveness. A complementarity analysis of the world's bumble bee *Bombus sibiricus* group was run to establish priority areas out of 120 equal-area grid cells occupied by its members on the world map. By only analyzing species richness, Ecuador was selected first, but when evolutionary distinctiveness was weighted, China came first representing 23% of the group's taxonomic distinctiveness compared to 15% found for Ecuador. This clearly demonstrated that traditional taxon richness approaches to establishing conservation priorities had limitations.

Phylogenetic Diversity

Phylogenetic diversity or "PD" is a measure of the relative feature diversity of a phylogenetic tree or subset of taxa (Faith 1992a, 1994a, b). It does this by counting all the branches spanned by the set of taxa including the branches at the root of the tree. In doing this, PD represents the total evolutionary history of the taxa in question (Faith 1992a,b, 1994a,b) and has even been equated with evolutionary potential (Forest et. al 2007). The fundamental principle behind PD as optimal for conservation measures is that option value for the future increases with the number of unique feature or attributes represented by taxa that are conserved. An individual species is of greater value if it contributes more novel features to a given subset of taxa and thus increases the overall biodiversity protected (Faith 1994b). In this model species are not given equal value, instead evolutionary distinction is measured by using phylogenetic theory to observe phylogenetic pattern and calculate the expected feature diversity of sets of taxa (Faith 1992b).

Figure 5: PD, a solution to an old debate?



This approach seems to provide the best solution to saving the cradle versus the museum debate. Instead of focusing on preserving one or the other, A,B,C or X,Y,Z type lineages (Figure 5), a PD approach to conservation is focused on preserving at least one minimum representative member of each lineage that represents a significant branch length of evolutionary history (See brackets, Figure 5). Thus if we lost all the branch tips represented by the X lineage we would still lose a significant amount of evolutionary history since they share a deeper root. Preserving at least one member of the lineage is preferable.

Few if any have called this new approach into question since its development in the 1990's. It is still a new approach and studies are just beginning to come out demonstrating powerful applications of the theory in the field of conservation. Sechrest et al (2002) demonstrated for carnivores and primates that previously identified global biodiversity hotspots have even greater amounts of evolutionary history than expected by measuring species richness alone. The study demonstrated that at the bioregion level evolutionary history, like taxon richness, is concentrated in disproportionately small areas. It was estimated that one third of the evolutionary history of all primates and carnivores is completely encompassed within hotspot regions. This study gives even more precedence to hotspot science at the bioregion level. A recent study however demonstrated something different at a finer, more local scale.

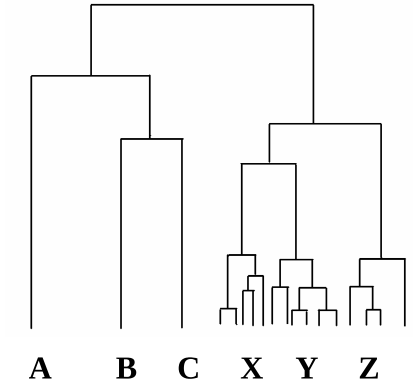
Forest et al (2007) demonstrated for the Cape Flora of South Africa that complementary gain of taxon richness and phylogenetic diversity were decoupled. This indicated that traditional approaches of prioritization based on taxon richness over-looked hotspots of important evolutionary history. Further more, they demonstrated that using a PD approach conserved the maximum amount of anthropogenic useful features for the future.

Davies et al (2007) ran a global PD analysis for parrots and found that the highest PD for parrots in SE Asia was in monsoonal rather than ever-wet rainforest regions. The monsoonal forests in this region are noted for generally having depauperate species richness compared to that of the wet regions. Davies et al. (2007) conclude by suggesting that ambient energy is the strongest predictor for PD, and that areas with high ambient energy correspond to seasonal tropical environments characterized by relatively low speciation and extinction rates. This study demonstrated another example of how taxon richness does not always correlate with PD.

Of particular relevance is the use of PD for prioritizing areas that should be added to existing reserves. Woinarski et al (1996) demonstrated how applying PD theory to a complementarity approach in the Northern Territory of Australia could do this. Instead of viewing areas that are proposed for conservation as isolated systems, this approach calculates the PD gain, or evolutionary potential gained, by adding particular areas over others to the entire reserve system by first calculating the PD of the existing reserve. This method of analysis is highly appropriate for areas that are divided among different land holdings with different degrees of conservation status. New computer programs such as the one applied in the latter case, DIVERSITY (Faith & Walker 1993) are constantly being devised and improved to make this type of analysis easier. Faith & Baker (2006) put it quite simply, that today the study of biodiversity is "fundamentally about information challenges."

With computers we can calculate unknown variations within the lineage of a given subset of taxa and more importantly compare taxa objectively in a way that allow us to side-step current debates about what is or is not a species (Faith 1992a; Mace et al 2003; Faith & Baker 2006). All biologists and taxonomists are familiar with the constant flux of species names and concepts. Since PD simply measures the branch lengths of representative taxa as indicated from molecular data, the names of the tips of the branches is generally irrelevant. In Figure 6, lineage Y may represent six species to one taxonomist, two species to another, and yet three to another taxonomist, but the PD value represented by the lineage will remain the same. For any taxonomists that have encountered the name shuffle problem, this fact alone makes the application of PD theory very promising.

Figure 6



Biodiversity conservation planning has traditionally been entirely sensitive to species definitions however recent work with PD is indicating that more robust information regarding overall biodiversity patterns may be found in phylogenetic patterns instead of potentially contentious species names. This has called for an increased effort in barcoding programs for measuring and sampling biodiversity (Faith and Williams 2005; Faith & Baker 2006).

The development of these methods suggests the potential for web-based PD analysis tool linked to the barcode-of-life data system (www.colbank.uoguel.ph.ca/), which could enable rapid biodiversity assessment of areas or taxonomic groups without extensive field or lab work or rather enhance the value of field work by combining the data with a web database. The need for further development and evaluation of such combined analytical methods has been addressed (Bininda-Emonds 2004, Creevey & McInerney 2005) and is even more relevant when considering larger assessment across different taxonomic groups (Soltis & Gitzendanner 1999). Clearly this science is still in its early stages, and its greatest benefits to applied conservation are yet to be fully realized. As more studies emerge so will a bigger picture of how to interpret the differences in results for different taxonomic groups and from different levels of taxonomic hierarchy and geographic scale.

In summary, using taxon richness as an indicator of the state of biodiversity fails to recognize that species are not equal in their contribution to global and biological diversity option values for the future from an evolutionary perspective (Barker 2002). The IUCN (1980) stated that the value of biodiversity was in its option value for the future. PD has demonstrated that it is the most effective method of achieving maximum option value by maximizing unique features of evolutionary history. However, PD has yet to gain prominence in the field of applied conservation and has received even less application in the field of resource management (Barker 2002). Additional studies in this field are needed. Finally and certainly not least, PD as an approach to biodiversity prioritization is not advocated at the exclusion of other methods (Barker 2002), as was clearly demonstrated by Forest et al (2007). PD used in conjunction with traditional approaches produces the most promising and useful results for biodiversity conservation.

Aims and significance of the present study:

The world's biodiversity is skewed both in its distribution and documentation. Areas with the highest species richness are often some of the most poorly known regions with only baseline data available for comparative analysis. On the contrary some bioregions are thoroughly documented permitting statistically robust analyses that can identify biodiversity patterns and priorities for conservation. Thus the field of biodiversity conservation itself must not only prioritize areas to conserve but also prioritize what type of scientific research can best further knowledge in specific geographical areas to aid its cause. The present thesis, divided into two parts, addresses this imbalance of global biodiversity knowledge by tackling relevant current conservation issues for biodiversity at regional scales in both well-known and poorly known areas. Part I addresses the need for baseline inventory and alpha taxonomy in poorly known regions. Part II addresses traditional and new emerging methods for the analysis of biodiversity survey data at a fine scale in well-known regions. Case studies from three model bioregions are drawn upon, each with unique challenges that require addressing for applied conservation; Micronesia, the Queensland Wet Tropics bioregion, and the state of South Australia.

Part I focuses on Micronesia, part of the globally recognized Polynesia-Micronesia biodiversity hotspot, that to date has remained poorly surveyed and understood taxonomically. Part I has three major components. The first two components are focused on the synthesis of existing knowledge to aid conservation prioritization. Knowledge of species distribution data is synthesized to update species concepts, their endemic status, and diversity patterns followed by an in depth exploration on the assessment of their threatened status in the absence of population level data. The third component explores a new potential methodology for increasing the efficiency of field surveying biodiversity in poorly known areas.

Micronesia is comprised of approximately seven major archipelagos in the moist tropics of the western Pacific. The islands as a whole are notable for having exceptional richness of plant species diversity and endemism on the global scale yet knowledge of their respective floras is extremely limited. The present study fills a major gap by compiling the first checklist of endemic plant species for the bioregion. This base-line level of knowledge, alpha taxonomy, is one of the most neglected areas of biodiversity research. Here the importance of this line of research is emphasized for both on the ground, local conservation schemes and for updating the science of global biodiversity patterns. The results update current knowledge by highlighting the Micronesia bioregion as having one of the highest levels of plant endemism in the entire world. Prior oversight to this pattern is due to the lack of sufficient base-line biodiversity research. In such a region, conducting analyses on the complementarity of species or the evolutionary distinctiveness of areas within the region would have limited value due to the paucity of survey data available for analysis. Here however, it is shown that traditional alpha taxonomy research, although less appealing to modern and popular interests, can yield results with global significance.

Chapter 1 starts with the compilation of a checklist of the endemic plants of the Palau archipelago in the Western Caroline Islands, Micronesia. The paper includes a preliminary IUCN red list assessment for each species and discussion on the distribution of rare and uncommon plants on the archipelago. In Chapter 2, a much deeper look at the Palau endemic flora is presented extending through the archaeological and palynological record to the first arrival of humans on the islands. In this chapter the preliminary IUCN red list assessment from Chapter 1 is revised and a critique of current IUCN red list criteria is presented in the defense of small tropical countries such as Palau that struggle with data limitations to enable red listing of their endemic species. Through a new inter-disciplinary approach combining palynological, archaeological, and botanical data an alternative method of assessing threatened status of plant species in poorly known regions is suggested as an alternate but equally scientifically valid approach that can be utilized instead of the IUCN assessment process.

The synthesis of this dataset enabled an un-anticipated secondary outcome of equal importance for the field of biodiversity conservation in the Pacific. The anthropogenic origin of “savanna” vegetation in the Palau archipelago is supported by the available evidence from all three academic disciplines; archaeology, palynology, and botany. Similar patterns of forest decline following human occupation of Pacific islands evident in the current vegetation and historical record are undoubtedly to be found in other Pacific islands. This study enhances knowledge of landscape history in the Pacific and challenges the field of conservation to utilize historical evidence and integrate a longer-term perspective when assessing habitat decline, the health of ecosystems, and populations of species.

Chapter 3 expands upon the prior two chapters by extending the view on the Palau endemic flora to the entire Micronesia bioregion. A complete checklist of all endemic plants for Micronesia is presented with notes and discussion throughout the text regarding taxonomic knowledge and problems for the respective taxa. A brief comparative analysis of the patterns of plant species richness and endemism across the region and between other Polynesian archipelagos highlights Micronesia as the epicenter of plant endemism in the Pacific. Extension of this analysis across all island biodiversity hotspots recognized by Conservation International (2007) puts Micronesia onto the global spotlight with the highest number of endemic plant species per square kilometer. Further discussion is provided on the history of taxonomic revision in the region and the importance of progressing taxonomy research in the Pacific.

In Chapter 4, the essential problem highlighted in the previous chapters of poorly known floras is tackled with the presentation of a pilot study aimed to estimate species diversity from tropical forest plots using only DNA tissue samples. Such a method holds promise for development of future rapid biodiversity assessments in poorly known biodiversity rich floras. The study tested this logic using current DNA barcoding technology in two rainforest plots with known species composition from tropical northeast Queensland. The study demonstrates the possibility of estimating species diversity with high accuracy without prior taxonomic knowledge however also emphasizes several technical challenges that require to be addressed for the technology to be utilized widely by non-experts.

In Part II, refined biodiversity analyses are presented from comparatively well-known floras. This section of the thesis is divided further into two components; 1.) The analysis of biodiversity survey data at the level of species and genera where the taxon is the unit of measure and 2.) The analysis of biodiversity survey data at the molecular level where feature diversity or genetic distance is the unit of measure.

The first component is addressed from a case study from southwestern South Australia in a bioregion that spans Mediterranean to semi-arid and arid environments. South Australia is considered the optimal location in Australia for addressing component one from Part II. The state of South Australia, although not often globally or nationally recognized for its levels of terrestrial biodiversity, maintains a systematically inventoried biological survey dataset that is unparalleled in Australia and of international noteworthy status. The databases contain approximately 1.5 million vertebrate records and over 1 million flora location records, which were all surveyed using the same methodology allowing statistically robust comparative analysis of the data. The exhaustiveness of this survey effort enabled a highly refined analysis, presented in Chapter 5, of the biodiversity patterns across a significant geographical area for all vascular plants, birds, reptiles, and mammals.

The aims of Chapter 5 were conceived in response to a conservation policy currently in development in the state of South Australia. A network of biological corridors called Nature Links has been proposed to be established throughout the state to link up intact areas of vegetation in combat of habitat fragmentation and to mediate the impacts of climate change on the migration of species' natural ranges. The present study utilizes species level data at a fine scale to assess the scientific value of the chosen corridor boundaries and essential logic behind conservation strategies that aim to increase connectivity as a default approach without reference to observed biodiversity patterns in the landscape. The results emphasize the importance of using traditional biodiversity indices to inform and guide conservation policy and the sheer value of collecting and maintaining highly refined species level distribution data. The results of this study have already proven to be influential within the government and academic sectors in South Australia and will hopefully influence long term state and national decision making strategies that are founded from a stronger link between science and policy.

South Australia has the opportunity to utilize its current Nature Links initiative as a global standard and success story. The State contains several nationally threatened ecosystems, high levels of nationally threatened species, and is projected to undergo some of the most significant impacts from climate change in the nation. Climate change has already made its presence tangible in South Australia and many ecosystems are already in severe decline. Thus although species richness may not be of global status and priority in this bioregion, the lessons and key messages inferred from this case study are applicable and relevant to all policy makers and conservation biologists working to maximize biodiversity conservation outcomes.

The second component of Part II is addressed in Chapter 6, which forwards the literature on the use of Phylogenetic Diversity (PD) for informing conservation decision making strategies. The study presents the largest to date phylogeny of tropical plants for an entire biome. The Queensland Wet Tropics was chosen as the ideal location for this study as it is arguably the most intensively studied tropical rainforest bioregion on earth however molecular studies on the flora have been extremely limited in comparison to many faunal groups. In addition, application of PD analyses for plants in the tropics has also been limited. The results identify hotspots of evolutionary history for this World Heritage recognized bioregion and identify the correlating patterns with hotspots of species diversity or taxon richness.

The Australian Wet Tropics are the main centre of rainforest endemism and diversity in Australia (Adam 1992; Wardill et al 2008). This high concentration of endemism and biodiversity within a small area (0.2% of the land area of the country) increases the area’s vulnerability to environmental modifications both anthropogenic and natural. Recent modeling studies predict that the expected effects of climate change may result in substantial losses of biodiversity (Wardill et al 2008). Due to the combination of the Queensland Wet Tropic’s internationally recognized significance to the study of biology and evolution and the fact that it is well known and surveyed compared to other tropical regions, it provides an optimal case study for applying new methods that identify and prioritize important areas of evolutionary history.

The major outcome of this work is the identification of a clear linear correlation between PD and taxonomic diversity for tropical northeast Queensland. These results challenge previous assumptions that the use of species or genera richness indices for conservation planning may not maximize evolutionary history and suggest that their use is still scientifically sound and accurate. With the support of an exhaustive genetic dataset, such results are likely to have a large impact in the field of conservation due to the substantial costs and expertise required for conducting large-scale molecular projects.

This thesis addresses the essential value of biodiversity patterns in the landscape at different scales. Instead of focusing on one or two iconic or flagship species, the level of the biome is addressed objectively in all cases using different measures of richness as an index of value. The results simultaneously progress scientific knowledge at the taxonomic level and identify strengths and weaknesses of current state, national, and global conservation schemes. By drawing on contemporary topics from three separate geographic bioregions an accurate view is portrayed on not only the skewness biodiversity itself but also the skewness of its knowledge. It is hoped that this holistic thesis approach will encourage progress on all fronts of biodiversity knowledge including alpha taxonomy, species discovery, pioneering of new methods, utilization of traditional methods that remain effective, and the incorporation of new evolutionary history perspectives based on molecular data into conservation schemes.

AIMS:

~ Advance biodiversity knowledge at the alpha taxonomy scale in the region of Micronesia by determining the endemic status of all vascular plants.

~ Assess the degree of threat using existing knowledge of the flora of Micronesia and re-evaluate the suitability of the IUCN red list methodology for poorly inventoried regions.

~ Develop and test the feasibility of a new rapid DNA barcode based biodiversity inventory method for estimating species richness.

~ Using standard biodiversity indices in a well inventoried region, assess how well an existing reserve system maximizes biodiversity representation.

~ Forward the literature on using phylogenetic diversity to guide policy by assessing how well phylogenetic diversity can predict taxonomic richness in a diverse tropical flora.

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PART I:
DIVERSITY AND THREAT OF PLANTS IN POORLY KNOWN LOCALITIES

CHAPTER 1

Plant Endemism, Rarity, and Threat in Palau, Micronesia: A Geographical Checklist and Preliminary Red List Assessment

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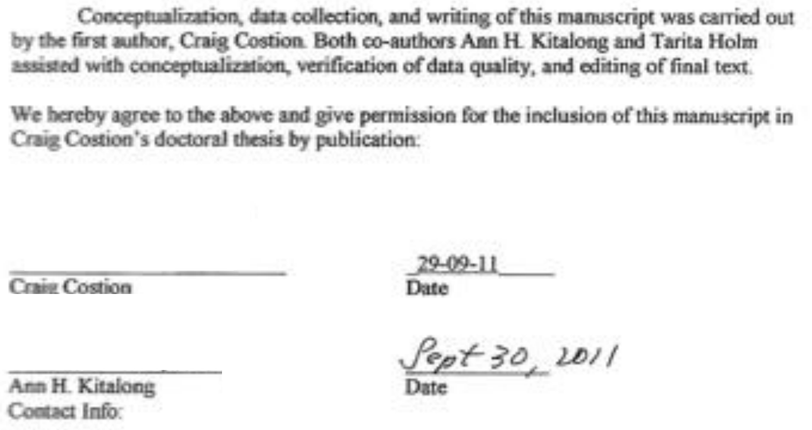
Micronesica 41(1): 131–164, 2009

Declaration of authorship



Conceptualization, data collection, and writing of this manuscript was carried out by the first author, Craig Costion. Both co-authors Ann H. Kitalong and Tarita Holm assisted with conceptualization, verification of data quality, and editing of final text.

We hereby agree to the above and give permission for the inclusion of this manuscript in Craig Costion's doctoral thesis by publication:

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ABSTRACT

An official checklist of the endemic plant species of Palau has been long awaited, and is presented here for the first time. For each species a substrate limitation, growth form, and relative abundance is listed. In addition an IUCN red list assessment was conducted using all available data. For over half of the endemic species there is insufficient data to provide a red listing status however an expected minimum number of threatened plants out of the total is inferred. Approximately 15% of Palau's endemic plants are believed to be only known from the type collection and many more only known from a few collections. These taxa however may now be prioritized and targeted for future inventory and research. The taxonomic robustness of several of these taxa is questionable and it is expected that more endemic species will be lost to synonymy in the future. Previous estimations have significantly over-estimated the rate of plant endemism in Palau (e.g., 194). Here, 130 plants are recognized for Palau, making its level of plant endemism comparable to some of its neighboring Micronesian islands to the east, notably Guam and Pohnpei. Several species are known to be restricted to isolated disjunct populations however the causes for their rarity are poorly known and have never been intensively studied. Palau although notable for its high percentage of remaining primary forest compared to other oceanic islands faces increasing threat from development making these small populations highly vulnerable. Nothing is known about how these rare species will respond to the imminent threat of climate change. There is no current legislation protecting specific plant species, as their rarity has never been systematically quantified. This paper represents a step towards plant conservation in Micronesia and it aims to stimulate further studies to address the data deficiencies documented here.

INTRODUCTION

The islands of Palau, lying roughly north of Papua New Guinea and East of the Philippines, contain a unique and rich flora that is shared with its neighboring islands to the east, the Caroline Islands, and the Marianna Islands to the northeast. This geographic region, known as Micronesia, comprises the northwestern part one of the 34 recognized biodiversity hotspots on earth (Myers et al. 2000). The Polynesia-Micronesia hotspot has been quoted as the “epicenter” of the current global extinction crisis. Palau at the western most boundary of this region is at a pivotal location. This tiny island nation, which is one of the newest countries in the world, as well as one of the smallest, has been noted for years by various authors in environmental evaluation reports for containing the highest rates of plant endemism out of all its neighboring island states in Micronesia.

This should be expected considering Palau by far contains the highest number of native plant species in Micronesia. Palau with a native vascular plant species count of approximately 724 species rivals its neighboring islands significantly. The numbers drop by over half traveling to the first island east with 376 in Yap (Fosberg et. al. 1979, 1982, 1987), then 328 in Guam (Stone 1970) and 357 in Pohnpei (Balick unpubl.). The numbers continue to drop rapidly traveling east to the Marshall Islands before reaching a vast blue expanse of ocean that stretches eastward to Hawaii. The flora of Micronesia is an attenuated flora deriving largely from the Indo-Malaysian region to the west. Conservation International (2007) declares a total of 3,074 endemic plant species in the region from western Micronesia across to southeastern Polynesia. The Office of Environmental Response and Coordination in Palau (2002) reported a total of 194 of these to be endemic to Palau, emphasizing that experts believe there to be more than this.

Where these statistics have been taken from and how they have been calculated has been one of the questions that have driven the author for the past several years. There has never been a checklist of endemic plants published for Micronesia. Throughout the course of the research presented in this paper, not only has the expected number of endemic species significantly dropped, but also the original assumption that Palau takes the limelight for plant endemism rates in Micronesia has been critically re-evaluated. The results presented here suggest that Palau may actually have the second highest rate of plant endemism in Micronesia, Guam being the first and that the neighboring islands have comparable rates to that of Palau.

Although the endemic statistics have remained obscure over time, the flora of the region is very well known in comparison to many other parts of the tropics. The prospect of finding new species, though clearly present, is relatively low compared to places such as Southeast Asia and the Neotropics. Progress on the flora of Micronesia began during the Japanese occupation of the region. Notable collectors included Hosokawa, Kanehirae, and Tuyama. Many of the current names accepted for Palau’s endemic plants were described by these pioneer botanists. Another early notable collector was Schlecter, a German botanist and orchidologist, who named many of Palau’s recognized orchid species. During the American occupation, work was continued mostly by Raymond Fosberg and his collaborators who described several new taxa, new combinations, and most of Palau’s endemic varieties. Although their geographical checklists (Fosberg et al. 1979, 1982, 1987) have proved to be an indispensable resource, it has also been a source of some confusion regarding which plants are endemic. In the Flora of Micronesia (Fosberg & Sachet 1975a, 1975b, 1977, 1980b; Fosberg et al. 1993), and other occasional publications on the flora of the region, endemic status is usually established. However these accounts are nowhere near a complete representation of the flora. What the geographical checklists lacked was a clear indication of which plants were actually endemic to the region. In the abstracts it is clearly stated how many of the plants listed are endemic to the Carolines, the Marianas, and endemic to the entire region but there is no further mention of endemism outside the abstract. The taxa presented in the checklist are not distinguished by these categories. The users have been left to determine this for themselves. This has lead to a great degree of error in calculating figures of plant endemism for some of the respective island states. For example, if a plant’s distribution within Micronesia is restricted to Palau, its distribution is listed as only occurring in Palau. This naturally has lead to assumptions that the taxa in question is endemic, when more often than not, its native distribution extends further west into Malesia. Many of these plants are at the eastern most limits of their native range in Palau.

An additional significant factor has contributed to this problem. Over time, a significant number of the names published during the Japanese era and even recent times have become basionyms or synonyms for species with a wider geographical range. This trend continues today and demonstrates how the determination of species as endemic to the region has been obscured by the slow simultaneous progress on the flora of Malesiana where as noted above, the vast majority of Micronesia's plants are derived. In addition to this, there is even slower progress towards published monographs of families and genera from the region.

These floristic problems came to the attention of the authors while inventorying collections from Palau at overseas herbaria and revising the checklist of vascular plants for the country, and stimulated the beginning of an effort extended over several years, amidst other projects, to compile an accurate list of endemic plants for Palau. Simultaneous work has been carried out by other Pacific researchers for the islands of Pohnpei and Kosrae and plans are underway to update the checklist of plants for the entire Micronesia region. The discussion here is limited to the islands of the Republic of Palau, geographically defined as the western Caroline Islands, excluding the island state of Yap of the Federated States of Micronesia.

In addition to contributing to the taxonomic progress of the endemic plants it has been decided to do so within the context of conservation. The link between biodiversity conservation and endemism is indeed, as stated previously, at the "epicenter" of current discussion in the field of biology. This is especially so for small island nations where the threat of losing an endemic species is much greater due to very small population sizes and vulnerable ecosystems with unoccupied niches. These uneven island biotas, often without predators, can be easily exploited by invasive species. The link is put even more into the context of taxonomy when it is considered how limited funds and resources could be

misspent on taxa believed to be endemic that are actually widespread.
For these reasons a preliminary assessment for the taxa represented here was done using the IUCN Red List criteria (IUCN 2001). For the majority, data has not been sufficient for establishing even preliminary status. It is hoped that this will not detract from the value of this checklist but instead stimulate effort and funding for a complete and thorough study to produce a complete red list assessment of Palau's endemic plants.

Lastly, it is expected that as new taxonomic treatments are published, this list, and naturally the statistics of endemic species for Palau, will continue to change. Many of Palau's endemic plants are poorly known and in some cases only by the type specimens or a few additional collections. Critiques on the taxonomy and endemic status of taxa listed here are welcomed and encouraged.

METHODS

Primary sources of information utilized include the working database in Palau referred to as the Palau Vascular Plants Database (PVPD 2006), the Provisional Checklist of the Plants of Palau (Kitalong et al. 2008), and Fosberg et al.'s checklists (1979, 1982, 1987). All species previously listed as endemic in any of the above checklists were critically assessed to verify their status. In addition, Fosberg et al.'s lists were reviewed systematically to check for any possible endemic taxa excluded from the former lists. The task of assessing endemic status began during herbarium inventories at the Bishop Museum. Any taxa listed as endemic with specimen records found in other countries were simply crossed off the list. This effort was later continued with a thorough literature review and inventory of digital herbaria and taxonomic databases worldwide.

The following databases were consulted for distribution records and the most up to date taxonomy: GBIF: Global Biodiversity Information Facility website: http://data.gbif.org/ welcome.htm (accessed August 2007) Kew World Checklist of Selected Plant Families. Royal Botanic Gardens Kew, online resource http://www.kew.org/wcsp/home.do (accessed August 2007) ILDIS: International Legume

Database Information Service. School of Plant Sciences, University of Reading. Website http://www.ildis.org/ (accessed August 2007) IPNI: International Plant Names Index website: http://www.ipni.org/ index.html (accessed August 2007) HUH: Harvard University Herbaria website: http://www.huh.harvard.edu/ (accessed August 2007) If the name and its distribution information were not found in one of these databases, often by conducting an online search, publications or articles that mentioned the taxa were found, from which distribution records were often obtained. If the plant occurred in other countries, then usually the search engine identified several links. For most of Palau's confirmed endemics, there were very few if any links found. In addition, for each family and genus that occurs in Palau, a search was done for any published monographs using the library resources at the Royal Botanic Gardens Edinburgh. The Flora of Malesiana was also thoroughly reviewed which was relevant to many of Palau's taxa. In most cases, if a taxa recognized by Fosberg et al. (1979, 1982, 1987) was reduced to synonymy in the Flora Malesiana, the Flora Malesiana was followed. In some cases however, Fosberg et. al's treatment (1979, 1982, 1987) was retained.

Only species found to be endemic to Palau are listed. Anything not listed here has been found to have distributional records outside Palau. Geographic data within the Palau archipelago was obtained from two primary sources; Fosberg et al.'s (1979, 1982, 1987) checklists and the author's database of over 14,000 plant collection records from Palau. This database was compiled from all databased herbarium specimens collected in Palau that are held at the Smithsonian herbarium (US), the Bishop Museum herbarium (BISH), and the Belau National Museum, in addition to presence/absence records obtained from the Babeldaob Forest Survey in 2005 (Costion & Kitalong 2006). Several cases proved that this supplementary data was worthwhile by extending the distributional ranges presented in Fosberg et al. (1979, 1982, 1987).

Symbols

(*) A "*" is applied following the name to indicate the particular taxon was either insufficiently represented or not represented at all in the author's database and its substrate restriction data (volcanic, limestone, generalist) was determined solely from the literature. A complete list of the literature consulted for distribution data is as follows: Hartley (2001); Hassler et al. (unpublished world checklist of Orchidaceae); Holttum (1977); Huynh (1999); Fosberg & Raulerson (1990); Fosberg & Sachet (1979, 1980, 1981, 1987, 1991); Fosberg et al. (1979, 1982, 1987, 1993). The lack of specimens from inventoried herbaria suggests that these taxa are relatively poorly known, although it is known that un-databased material exists at the Smithsonian and the University of Guam, but was not seen by the authors. Until these records are databased, they remain unavailable for analysis.

(+) A “+” is listed after the name to indicate that the taxon is only known by the author from the type specimen or otherwise a single collection, or even in some cases where no specimen at all could be located. This serves to highlight taxa *very* poorly known and in need of further collections. Distributions of these taxa were determined from the checklists of Fosberg et al. (1979, 1982, 1987) and/or from the protologues or type specimen labels.

IUCN Red List Status

All species listed have been assessed using the IUCN Red List categories and criteria (IUCN 2001). Taxa recognized as endemic only to the varietal rank, have not been assessed. Abbreviations used for the categories are as follows:

CR: Critically Endangered
EN: Endangered
VU: Vulnerable
NT: Near Threatened
LC: Least Concern
DD: Data Deficient

Categories that classify as threatened are highlighted in bold. If a taxa meets the criteria for one of the threatened categories, then the specific criteria that it qualifies under is listed in parenthesis following the IUCN red listing format (IUCN 2001). For example, *Cycas silvestris* K.D. Hill, **VU**(D2) is an Australian cycad that qualifies as **vulnerable** under criteria D2 which states that the area of occupancy must be less than 20 km^2 or the number of locations is less than or equal to five. This species is restricted to the Cape York Peninsula, Queensland and only known from a few small stands that lack adequate protection (Hill, 1992). The specifications of the categories criteria are easily obtained from the IUCN website (www.iucnredlist.org) and will not be repeated here.

Growth Forms

Eight growth forms were abbreviated as shown below. Some species have more than one form.

T = Tree
T(u) = understory tree
T(c) = canopy tree
S = shrub
L = liana
HP = hemi-parasite
H= herb
E = epiphyte

Relative Abundance Codes

This category was determined roughly from overall knowledge of the authors' field experience, data records, and review of the literature. It is included to help distinguish between different types of rarity. Plants that are uncommon to rare but across the island, plants that are locally abundant but restricted to small localities, and plants that are widespread. Code abbreviations are as follows:

R = Rare, very uncommon or very poorly known
RR = Range restricted, only known to specific localities
U = Uncommon, but found throughout the substrate type
C = Common, widespread in occurrence
A = Abundant, grows in abundance where found
D = Dominant, forms a dominant layer in the forest structure
DD = Data deficient, insufficiently known

RESULTS

A total of 130 vascular plant species are listed here as restricted to Palau with an additional 23 endemic varieties. Well over 100 plants that were considered potentially endemic in the PVPD were found to have wider distributions outside Palau. Most of these had ranges extending into Malesia and some shared their distributions with other Micronesian island states. Plant distributions within the archipelago can be divided into three main categories. Plants restricted to volcanic islands, plants restricted to limestone islands, and generalist plants occurring on both substrates. A few taxa are restricted to specific islands within these categories. A total of 75 species were found to be restricted to volcanic islands including one restricted to the island of Malakal in Koror; 31 species are restricted to Limestone islands including one restricted to Peleliu and one restricted to Angaur; 24 species are considered generalists occurring on both volcanic and limestone islands.

Species endemic to volcanic islands

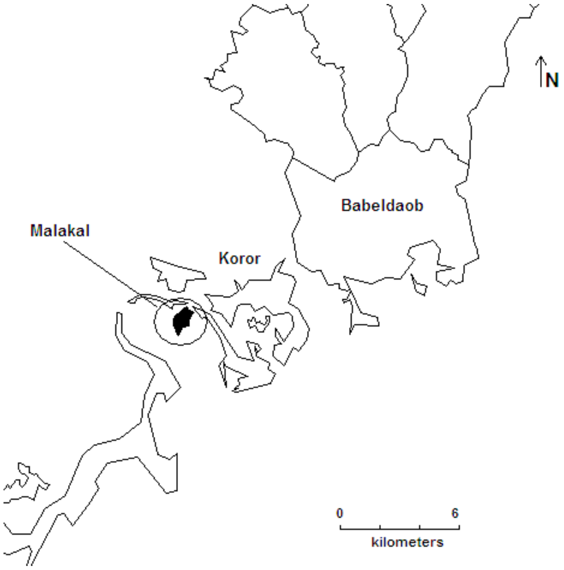
It is believed that the volcanic islands of Palau were formed beneath the ocean’s surface and were subsequently uplifted during the Miocene and Pliocene (Fig.1). Clay was formed from the erosion of upper exposed parts of the Island down into the swamps and coastal areas (Goldich et al. 1948). Today parts of the originally exposed basalt rock can be found scattered on the high ridges and hilltops of Babeldaob. Below these small areas it is mostly volcanic clay. Though the soils are acidic and nutrient poor, the total landmass of Babeldaob has produced high rates of plant diversity and endemism in comparison to other islands of Micronesia. Babeldaob is 331 km², making it the second largest island in Micronesia. The volcanic islands of Koror, Malakal, and Ngarekebesang although mostly urbanized, contain remnant patches of a similar flora to that of Babeldaob. The volcanic sections of Koror are virtually entirely deforested, though Malakal has some patches remaining. The island of Ngarekebesang contains the largest area that has not been developed on the volcanic parts of Koror and has not been intensively surveyed.

Figure 1: Volcanic islands, Palau

A total of 75 vascular plant species and 12 endemic varieties are listed here as endemic to Palau’s volcanic islands. The majority of these are expected to be found only on Babeldaob, however many do have ranges that extend to the volcanic islands of Koror state. Since it is difficult to presume exactly how similar the original vegetation of the Koror islands was to Babeldaob, prior to human habitation, it is most logical to treat all the volcanic islands as one floristic unit. There are a total of four endemic fern species, three *Sellaginella* species, and 68 endemic angiosperm species. Families most strongly represented are the Orchidaceae with a total of 21 species, Rubiaceae with eleven, and Pandanaceae with five. Only one plant is known with a range restricted to a volcanic island in Koror. *Timonius salsedoi* is only known from the island of Malakal (Fig.2).

Described by Fosberg & Sachet (1987) this plant is only known from the type specimens and is poorly known. No information has been recorded regarding the population size or ecology. However, the amount of suitable habitat on this island qualifies this species under the class of Critically Endangered, under the IUCN red list guidelines. Malakal is a very small island with less than half of its land area providing suitable habitat for native vegetation. This small area is restricted to patches on top of the island's hill and fragmented from subsistence farming. The island is heavily developed along the coast at the bottom of the hill and the vegetation at the urban boundary is occupied by introduced and invasive species. Currently there is no known legislation to protect the remaining areas of vegetation on the hill. The occurrence of this threatened species warrants protection of all remaining forest on the island until further studies can be undertaken. Collection of population data on the island of Malakal for this species is highly recommended. A phylogenetic study of the genus *Timonius* in Palau would be beneficial to confirm it is a distinct species and not merely a regional variant of another more widespread species. To date, no other species have been described as restricted to any islands as small as this one in Palau.

Figure 2: Malakal Island



Species restricted to limestone forest

The limestone islands are derived from lime-secreting organisms that flourished in tropical seas that became shallow from the volcanic eruptions forming Babeldaob and Koror. These deposits have likely been continuous since the Miocene. Parts of southern Babeldaob are actually limestone formed from these deposits (Fig. 3). The high limestone islands, known today as the Rock Islands, are older, formed from the Miocene to the Pleistocene and were also subject to significant uplift (Goldich et al. 1948). There are between 250 and 300 islands with a total area of 47 km². They are composed of karst limestone, which is jagged, and sharp making it dangerous to traverse. Early Palauan settlers were known to inhabit these islands but they have long since been abandoned and are now virtually all undisturbed virgin forest. The vegetation here is distinct with virtually no topsoil. The plants often literally cling to shear rock. Some of the endemic plants are restricted to the karst Rock islands, but many also occur on the low platform islands to the south. The low platform islands and reef atolls such as Peleliu, Angaur, and Kayangel, are younger, believed to be formed from deposits from the Pleistocene to recent times (Goldich et al. 1948). Peleliu and Angaur are lower and generally flat islands that have undergone heavy disturbance particularly in the 20th century, and are currently inhabited.

Figure 3: Limestone Islands, Palau

A total of 31 endemic species and seven endemic varieties were found to be restricted to the limestone islands of Palau including four ferns, two palms, three orchids, and four members of the Rubiaceae family. The remaining families are represented by only one to two species. Families that occur here, but are not represented on the volcanic islands by any endemic species, include Lomariopsidaceae, Arecaceae, Caparidaceae, Cucurbitaceae, Elaeocarpaceae, and Vitaceae.

Due to its inaccessibility the Rock Islands are relatively undisturbed, however they are also poorly studied. It is expected that most of the taxa listed here be distributed throughout the limestone islands though with some restricted to the Rock Islands. Further studies are needed to determine the degree of abundance or rarity and assess the degree of threat proposed to many of these plants. One endemic palm, *Ponapea palauensis* is considered critically threatened as it is restricted to a few Rock islands and of the three areas where it has been found only one has a healthy stand of trees (Lewis 2008). A second endemic palm species, *Hydriastele palauensis*, is more common than the former, though only occurring in scattered patches throughout the Rock Islands. Both palms are considered threatened by two species of introduced parrots (Mueller- Dombois & Fosberg 1998). Manner and Raulerson (1989) documented the continued plight of *Hydriastele* in the Seventy Islands reserve, which was once believed to provide a refuge for the palm, emphasizing its continuing decline. Follow up studies have been limited.

Species restricted to Peleliu

Peleliu is one of the largest limestone islands in Palau, with a total land area of 13 km², and is the most populated with approximately 700 inhabitants (Fig.3). The island is most notable for being the site of a major WWII battle, the Battle of Peleliu. From what is currently known, there were not many endemic plants on the island to begin with. Local lore asserts that after the battle, only one coconut tree was left standing. Today the untrained eye would never be able to tell, as it is quite heavily forested. However the majority of the vegetation is secondary regrowth and has become dominated by the non-native *Timonius timon*. One endemic species, *Pandanus peliliuensis* Kaneh., is recognized as being restricted to Peleliu (Fosberg & Sachet 1987). This taxa is only known from isotype specimens (HUH, NY), which are only fragments. Further collections are needed to verify to what extent it occurs on the island and quantify its population size.

Species restricted to Angaur

Angaur is positioned further south from Peleliu and across an ocean channel (Fig. 3). Unlike the rest of the archipelago discussed here, which occurs within a sheltered coral lagoon, Angaur is surrounded by open ocean. It has a land area of 8 km² and a small population of less than 200. The island was also a WWII battle site, and was mined for phosphate from 1909 to 1954. It is likely to have experienced much disturbance in the past century but today is mostly forest. One endemic plant is currently recognized as being restricted to Angaur; *Maesa canfieldiae*. The authors of this species (Fosberg & Sachet 1979) however note that the plant has only been known to the local inhabitants after WWII and could have possibly been introduced from elsewhere. They further document that the plant is closely related to *Maesa tetrandra* (Roxb.) A. DC. and *Maesa papuana* Warb., which occur in Papua New Guinea and the Malesian region, though it doesn't match either of them exactly. It has tetramerous flowers like the latter two, unlike all the other Micronesian species, which have pentamerous flowers. The Myrsinaceae family has to date not been treated in the Flora Malesiana. Until this has been done, or other studies indicate otherwise, the name *M. canfieldiae* will be retained.

Generalist endemics

The following 24 endemic species occur on both volcanic and limestone islands of Palau. They are all angiosperms. Families not represented by species in the volcanic and limestone restricted categories include; Anacardiaceae, Celastraceae, Flacourtiaceae, Myristicaceae, Myrtaceae, Olacaceae, Piperaceae, and Putranjivaceae, suggesting that the taxa represented by these families may have better dispersal capabilities and/or less habitat specificity within the archipelago. Most of them are widespread, common species and unlike the former categories, few are poorly known.

Candidate endemics

Two species are listed as candidate endemics due to considerable doubt over their taxonomic status as separate species. A brief summary of the known information regarding them is provided. *Limnophila palauensis* T. Yamaz; possibly same as *L. indica* var. *raymundii,* which also occurs on Guam. The author of the former did not view the type of the latter when describing the new taxon (Yamazaki 1993), and some of the characters used to distinguish them are questionable. If it is distinct however, then it is endemic to Palau. Further study is required. *Decaspermum raymundii* Diels Both Fosberg et al. (1979) and Stone (1970) doubted that this was distinct enough from *D. parviflorum* (Lamarck) A. J. Scott to validate the application of a separate species name. However, Scott (1979) accepts the name and lists it as endemic to Babeldaob. The former authors were the most experienced in the flora of the region, however the later author specialized in this genus. Further study will enable its delimitation with confidence.

Endemic varieties

A total of 23 endemic varieties are recognized here from 12 different angiosperm families. In all families except the Rubiaceae, there are only one to two endemic varieties. The Rubiaceae has nine recognized endemic varieties with four represented by the genus *Psychotria* and four represented by the genus *Timonius*. A total of 17 of the 23 varieties were described by Fosberg and Sachet. All the names presented here are recognized in the current literature. However, it is reasonable to expect that some will become synonyms after monographs of the respective genera are completed. The regional variation that Fosberg and his colleagues often used as a basis for splitting taxa is sometimes viewed differently by authors of monographs that study genera across a larger distribution.

Rate of endemism

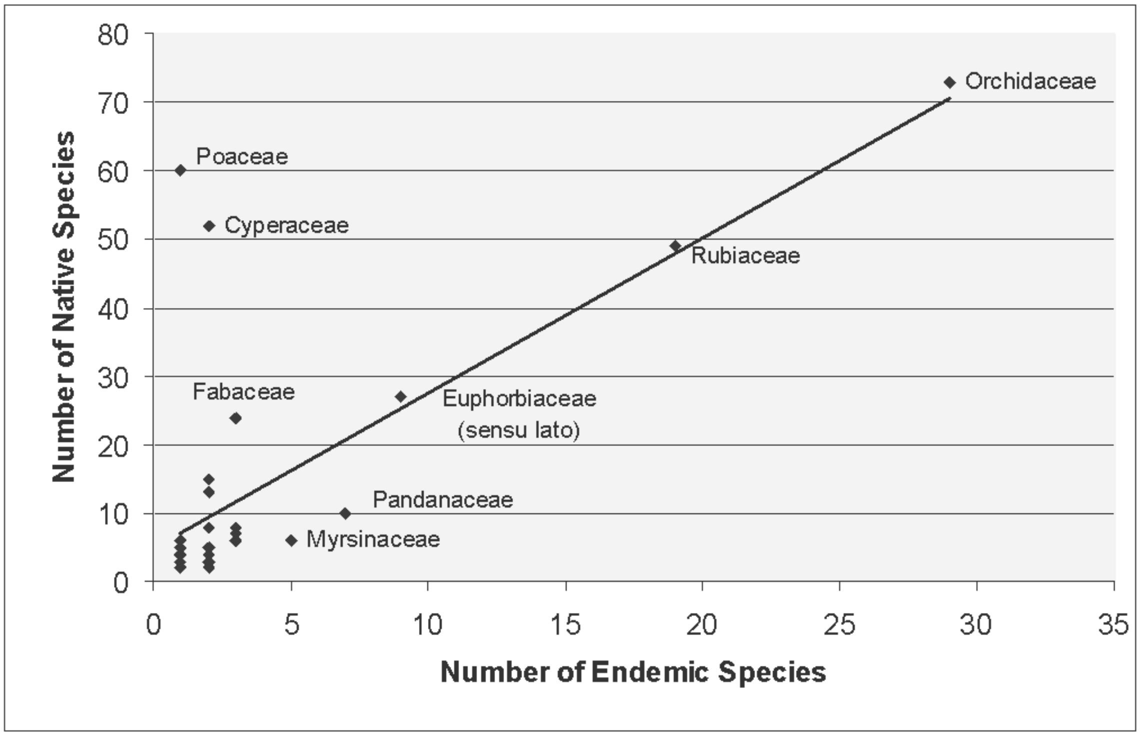
Figure 4 shows three different trends. Each data point represents one of the families represented in the checklist of endemic species. The vast majority of families are low in both numbers of native species and endemic species, with no obvious reciprocal relationship between the number of species and number of endemics (Fig.4). These families often have high rates of endemism at the family level (see Table 1). This is likely the result of few representative species being dispersed to Palau in addition to relatively low rates of species radiation. The Orchidaceae, Rubiaceae, and Euphorbiaceae (*sensu lato*) however demonstrate a trend of endemism being directly proportionate to an increase in the number of native species. These families are notable worldwide for high rates of species diversity (Judd et al. 2002). The percentage endemism for these families in Palau (Table 1) is significantly lower than families such as Annonaceae and

Myrsinaceae, the high relative endemic species richness in these later three families is likely a combination of higher rates of successful dispersion of native taxa to the islands and high rates of insular speciation.

Wind dispersed taxa, including the Poaceae and Cyperaceae, although high in species richness, have the lowest rates of endemism. The same is true for Asteraceae, which has no endemic species in Palau. Wind dispersal, allowing propagule movement between Pacific islands, is likely a significant factor contributing to this. There is also palaeoenvironmental evidence to suggest that the abundance of these groups, particularly the Poaceae and Cyperaceae, is a recent occurrence in Palau. Athens & Ward (2002) showed from sediment core analysis that savannas and pollen from savanna indicator plants either do not appear in the sediment record at all or are very limited prior to the colonization of humans and forest clearing. The sudden appearance of Graminoid pollen suggests that many or some Graminoid and even Asteraceae taxa may have dispersed to the islands more recently after the expansion of suitable habitat following human disturbance.

Figure 4 appears to provide some support for the recent theory of "diversity begets diversity" (Emerson & Kolm 2005a, b), which suggests high rates of species diversity foster higher rates of speciation and endemism, particularly on islands. However, clearly for wind-dispersed taxa this model does not apply. There are also additional outliers evident in Figure 4, notably the Myrsinaceae, Pandanaceae, and Fabaceae that don't strongly support this model. The skewness of biodiversity has been well documented for both taxonomic groups and geographical locations (Pimm et al. 1995; Purvis et al. 2000; Sechrest et al. 2002). The data presented here seems to support the "diversity begets diversity" theory primarily for taxonomically skewed families, i.e. those prone to high rates of speciation. The remaining families do not appear to follow any obvious trends on the whole.

Figure 4: Number of endemic species in proportion to number of native species



The majority of endemic plants in Palau are trees, comprising 38% of the total, followed by herbaceous terrestrial plants with 28%. Shrubs and lianas together comprise 22% and epiphytes total to 12% (Fig. 5). These figures were compared to all native plants using the growth form categories from the Provisional Checklist of the Plants of Palau (Kitalong et al. 2008) in Table 2. Trees and shrubs have higher representation in the endemic species count compared to native plant tallies. This demonstrates a stronger trend towards endemism with arborous habit. However, epiphytes were not distinguished from herbs in the Provisional Checklist, thus they could not be compared. Due to the high rate of endemism in the orchids, epiphytes are also expected to have a high tendency towards endemism whereas terrestrial herbs, abundant with graminoid species, are likely to have a lower percentage.

Plant endemism on limestone islands, when calculated per square kilometer (34%), is significantly higher than on the volcanic islands (21%), where the majority of endemics occur (Table 3). To explore the reasons for this thoroughly and adequately requires further investigation and comparison with other islands across the region, which shall be left for subsequent publications. This data may however suggest support for the general dynamic theory and speciation pulse model for island biogeography of Whittaker et al. (2007, 2008). This model considers island age to have primary importance in species diversity and endemism on islands. New islands increase in diversity and endemism with time but only to a certain point at which opportunities and niches for evolution and radiation diminish through time. The karst limestone islands are notably younger than the volcanic islands.

Figure 5: Growth forms of all endemic Species

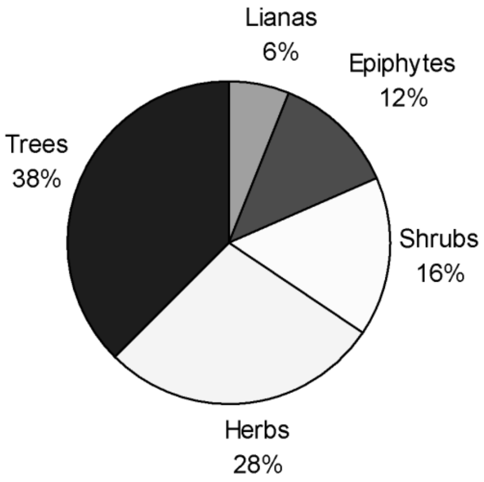


Table 1: Percent Endemism of Selected Families

Family	Native Species	Endemic Species	Percent Endemism
Annonaceae	2	2	100%
Gesnariaceae	2	2	100%
Myrsinaceae	6	5	83%
Pandanaceae	10	7	70%
Melastomataceae	3	2	67%
Sapotaceae	3	2	67%
Orchidaceae	73	29	40%
Euphorbiaceae	27	9	33%
Fabaceae	24	3	13%
Cyperaceae	52	2	4%
Poaceae	60	1	2%

Table 2: Comparison of the distribution of different growth forms for native and endemic angiosperm species.

Flowering Plants	Trees		Shrubs		Lianas/ Vines		Herbs & Epiphytes	
Native	177	29%	71	12%	56	9%	301	50%
Endemic	49	41%	21	18%	8	7%	41	34%

Table 3: Percent endemism (E/km^2) for each island type (km^2 data for substrate types provided by USDA Natural Resources Conservation Service).

	Endemic Species (E)	Total Area (km^2)	% Endemism (E/km^2)
Restricted to Volcanic	75	363	21%
Restricted to Limestone	31	90	34%
Generalists	24	453	5%
Total for Palau	130	453	29%

IUCN Red List

There is insufficient data for 61% of Palau’s endemic species thus these species cannot be adequately assessed under the IUCN criteria (Fig. 7). These will remain as data deficient, “DD,” until further studies are done. There is sufficient data for the remaining 39%, of which 30% of these, or 39 species, were of “Least Concern” because they were either common or widespread. Five endemic species (4%) are considered near threatened, three species (2%) are considered vulnerable, and the last two categories, critically endangered and endangered are each represented by two species (1.5%). If this 39% is considered a representative sample of all Palauan species, we can make an estimate of the IUCN categories for the 61% of data deficient taxa and the entire endemic flora. The percentages of the species with sufficient data are shown in Figure 6. If we assume that the data deficient taxa follow a similar proportion of rareness then it can be estimated that there would be approximately 99 species of least concern, 13 species of near threatened, eight vulnerable species, five endangered, and five critically endangered endemic species for Palau. This is a very conservative estimate, as many of the species considered of least concern are taxa that are well known. It is more likely that there will be a higher proportion of threatened species represented from the Data Deficient category listed here. Many of Palau’s poorly known taxa may be rare or have restricted ranges. Indeed a total of 19 (15%) are only known from the type collections. An estimated minimum number of endemic plants expected to be threatened in Palau is inferred as shown in Figure 7. This was calculated by excluding the data deficient taxa then recalculating percentages for all known taxa. The 39 (30%) LC taxa become 76%, which is then multiplied by 130, the total number of endemic species equaling 99. The minimum expectation is the sum of 8, 5 and 5 (VU + EN + CE in Figure 7), 18 species (14%). An additional 1% is added to give the greater benefit of doubt considering this is a conservative estimate. This produces an estimation of 20 (15%) out of the total of Palau’s endemic plants. It is stressed that this is the estimated minimum that may be considered threatened following more thorough studies. By the time these studies are done, there may very likely be additional or increased threats.

Previous results produced by the author (Costion 2007) demonstrate that this may be a relatively accurate expectation. Turnover, or β diversity, for the island of Babeldaob was calculated using DIVA-GIS. The results clearly suggested that most of Palau's endemics are widely distributed across the island, with a small percentage that have small restricted ranges or disjunct distributions.

The results showed a significant difference in β diversity for all native species compared to the β diversity for endemic species only. Clearly, the endemic species formed a more consistent component of the vegetation across the island as a whole, with a small turnover rate, whereas the same analysis for native species showed a higher turnover rate. Six endemic trees are known to have rare and restricted populations including *Ponapea palauensis*, mentioned above. *Parkia parvifoliola* is only known from one healthy population with two scattered individuals adjacent to this area and three disjunct individuals recorded further south. *Terminalia crassipes* is a riparian tree only known to occur along two of Babeldaob's river systems. *Rauvolfia insularis* occurs in very small numbers with a scattered distribution. *Goniothalmus carolinensis* is a poorly known species that has only been recorded from a few collections on Babeldoab. Kitalong (2008) documented the occurrence of *G. carolinensis* on the limestone islands. This data however could not be sourced or verified so it remains listed as restricted to the volcanic islands. *Manilkara udoido* is abundant and can form a dominant understory canopy where it occurs, but its range is restricted to the southern portion of Babeldaob with the exception of a few disjunct individuals. The causes of population disjunctions for all of these trees are unknown.

Figure 6: Percentages of all plants assessed for each IUCN red list category

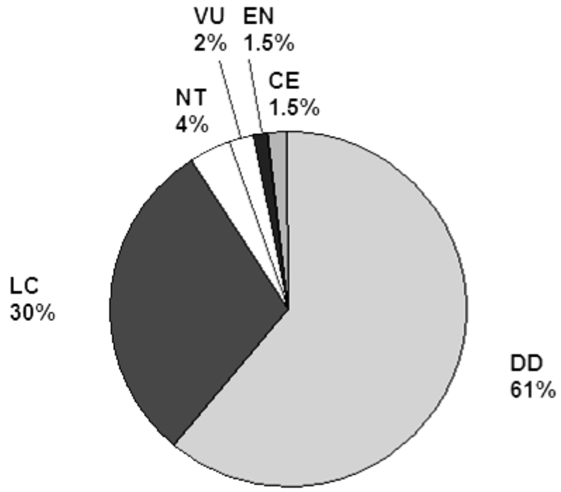
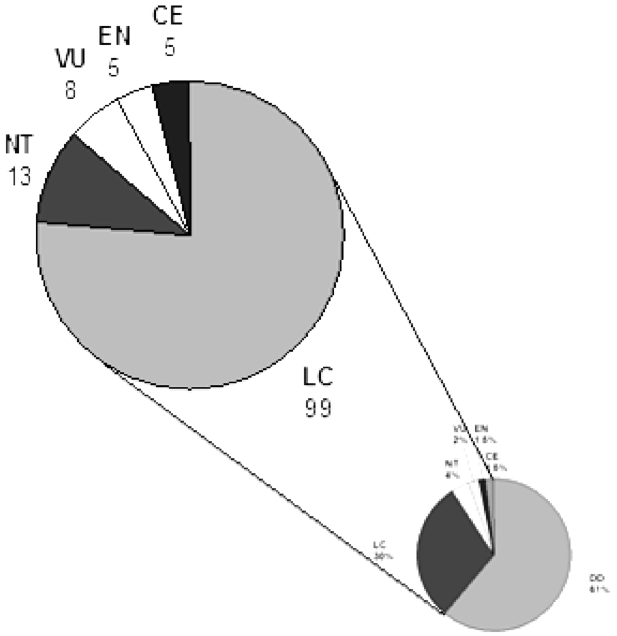


Figure 7: Percentages inferred from the total of assessed taxa with sufficient data. The lower pie is the same as that in Figure 6.



Biogeographic comparison

A total of 724 plants are listed as native or endemic in Palau's latest checklist (Kitalong et al. 2008). If the total number of endemic species, 130, is divided by this figure then Palau has a rate of endemism calculated by number of endemic spp. (E/N), of 18%. Calculated per sq. km for the total land area, 458 km^2, the rate is 29%. These new figures are important in that is has been traditionally assumed that Palau has the highest plant endemism rates in Micronesia. Based on the revised data presented here Palau appears to not be significantly different from other Micronesian islands. Guam has a plant endemism rate of 21% (calculated by E/N) based on statistics from the Flora of Guam (Stone, 1970). This percentage exceeds that of Palau's. The list of endemic species for Guam however, may need to be updated as recent work in the Caroline Islands has clearly demonstrated. The number of accepted native and endemic species has significantly changed since 1970. Recent estimates for the eastern Caroline Islands (Balick unpubl.) indicate that Pohnpei's flora is only 1% lower than Palau (calculated by E/N) and Kosrae's flora is also only 1% lower (calculated by E/km^2) showing comparable rates of endemism to that of Palau's.

Distance from continental sources have clearly effected the richness of plant species in the islands of Micronesia, but does not appear to have affected equally the rates of plant endemism. Similar results are shown by (Keppel 2008, Keppel et al. 2009) where isolation is highlighted as a more significant factor contributing to plant endemism rates on oceanic islands in the Southwest Pacific. What factors then, are most significant in determining rates of plant endemism in the region; distance from source, island size, elevation gradients, or island age? A comprehensive biogeographical analysis and comparison of floristic data for each of the respective islands in the Micronesian region is now needed to explore these questions further. This should include updated checklists for native and endemic species for each island. Palau, Pohnpei, and Kosrae have all been recently updated and checklists are currently being finalized for publication. Updates are needed for Guam, Yap, and Chuuk.

Threats

Palau boasts 70% of its land mass covered by intact forest. On Babeldaob, it is difficult to discern areas that are actually pristine primary forest from forests regenerated from early Palauan disturbance however the limestone Rock Islands are the least impacted and contain areas virtually untouched. Their inaccessibility renders a comforting protection to them and they are one of the only areas remaining as such in all of Micronesia (Mueller-Dombois & Fosberg 1998). As a whole, Palau may be considered a “good news area” for Micronesia (Myers et al. 2000), with its high percentage of intact forest. For this to remain true prompt action must be taken as the island of Babeldaob, approximately 70 % of the total landmass of the archipelago faces increasing imminent threat from development.

Islands have historically been exceptionally vulnerable to extinctions. The IUCN determined that of all recorded extinctions for mammals, birds, amphibians, reptiles, and molluscs; 72% were island species (Baillie et al. 2004). This has been especially true for birds. Ricketts et al. (2005) document 245 extinctions from mammals, birds, selected reptiles, amphibians, and conifers that have occurred since 1500. Of these, 80% occurred on islands and more than one half were from tropical moist forests. The current percentage is now more balanced, but not due to a reduced threat on islands, rather an increased threat in continental areas (Ricketts et al. 2005; Baillie et al. 2004). Islands are still arguably at greatest risk. Of all the recorded extinctions that occurred after 1983, over half were from islands, the bulk of which were from Hawaii and Guam (Baillie et al. 2004). These extinctions render the Pacific as having more recorded extinctions over the last 25 years than any other biogeographic realm. This suggests that the Pacific islands may be one of the most threatened of all of Myers et al. (2000) biodiversity hotspot regions, or at least the most vulnerable to extinction.

Of the recent extinctions, 85% of species had restricted ranges. Commonly cited causes of extinction are habitat loss, invasive alien species, and overexploitation.

Of the recent extinctions post-1983, the most commonly recorded cause was habitat loss, followed by introduced species. Over-exploitation was not a significant factor in these recent extinctions (Baillie et al. 2004). This trend is similar historically and highly relevant in Palau. The primary threat to native vegetation historically in Palau has been forest degradation as a result of human activities. Palaeoenvironmental investigations conducted in Palau (Athens & Ward, 2002, 2005) provide convincing evidence that the island of Babeldaob was entirely forested prior to human colonization. After the first evidence of humans occurs in the pollen records, charcoal deposits as well as pollen from savanna indicator species; Poaceae, Pandanaceae, and Cyperaceae, rise significantly. These pollen types are absent or minimal prior to this. In addition, several unknown pollen types recorded from pre-human times rapidly decrease after human settlement. Some of them completely disappear and are no longer present in contemporary pollen profiles. Similar results have been shown for other Pacific islands. On the island of Kosrae, the entire lowland vegetation was replaced by agroforest within 500 years of human colonization (Athens et al. 1996). On the island of O'ahu, Hawaii a similar scenario has been shown although the causes are less likely to be due to direct clearing for agriculture and possibly related to the introduction of the pacific rat or other causes (Athens 1997, Athens et al. 2002). On the island of Guam, indicators of disturbance arise around the same time as Palau at 4500 to 4300 cal. BP. Ample evidence from additional islands throughout the Pacific support a similar scenario occurring at different times, all independent of climate change (Athens & Ward 2005).

This implies that not only has the extent of native forest been significantly reduced, but many current areas of seemingly "pristine" forest may actually be re-growth. Studies in Palau have shown (Endress & Chinea 2001) that the edges of forest do expand back into savanna areas if the savannas are left alone and not burnt. Further more, the evidence of "unknown" pollen types suggests the likelihood that some species may have either been significantly reduced in their area of occurrence or even gone extinct. This evidence raises many questions regarding the rare and disjunct distribution patterns of several of Babeldaob's endemic species discussed above.

Endemic plants that are rare or with very small restricted natural ranges, often restricted only to one hilltop or valley, are not uncommon in the tropics (Myers 1988, 1990). These localized endemics with very small ranges are well documented in the Neotropics and on islands (Gentry 1986; Cody 1986). These can be neo-endemics that have evolved more recently such as the case in Amazonia with the result of Andean uplift creating many new isolated habitats (Gentry 1982), or relict or palaeo-endemics which are often rare due to the loss of a former more widespread habitat such as has been suggested for many monotypic genera in the Australian wet tropics of Queensland (Bowman 2000, Kershaw et al. 2005, Greenwood & D. C. Christophel 2005). Alternatively they may be localized as a result of human activities and habitat loss.

The neo-endemic model proposed by Gentry (1982) implies habitat specialization. Although *Ponapea palauensis* is only found near depressions that are damp or near lakes in the Rock Islands and *Terminalia crassipes* is restricted to streams and rivers, their distributions are disjunct and restricted. Although not a complete explanation, as not all of the known rare endemics occur in specialized habitats, recent molecular work strongly supports the notion that much of the Pacific biota has evolved recently (Price & Clague 2002; Keast 1996; Keppel et al. 2008a, 2009, unpubl.). The palaeo-endemic model is unlikely due to the relatively young age of the islands. In any case, there is insufficient palaeoenvironmental data but the studies that have been done (Athens 1997; Athens & Ward 2002, 2005; Athens et al. 2002) do not indicate significant vegetation turnover prior to human settlement in the Pacific.

The relationship between the increase in charcoal and savanna indicators, as well as the loss of “unknown” pollen types at the time of human colonization, is suggestive of an anthropogenic cause of rarity. However, the mystery is far from solved. More data and studies are needed to support any of the above hypotheses for Palau. The causes of rarity in the tropics are a poorly understood and are an understudied topic. In any case it is indisputable that these plants are significantly threatened. Their habitats need only be destabilized or disturbed to put them at risk of “summary extinction” or secondary causes of extinction (MacArther & Wilson 1967, Myers 1988, MacKinnon 2005). Historically fire has clearly been the most effective method of forest clearing for Palauans, but this has become an increasingly pertinent issue today. Traditional systems of government that regulated the use of fire have eroded. Every year careless fires are lit and occasionally some get out of control and destroy patches of forest. Today however, fire is not the only threat to Babeldaob's remaining forest. The construction of the 53 mile Compact Road, which encircles the island, has opened Babeldaob up for development. Building the road was part of the Compact Free Association Agreement with the US, which granted Palau independence. In return for allowing the US military access to the island at anytime in the future Palau was granted the funding for the Compact Road, additional funding, and other benefits. There has been much written about this elsewhere. It is mentioned here only to highlight a potentially significant future threat. The construction of a US military base on Babeldaob would undoubtedly result in massive forest clearance and pose a serious threat to some of Palau's rare trees among other environmental problems. This has certainly been the case in Guam.

A national highway, which has very much been needed and appreciated by the island's inhabitants, has now for the first time made development on the island of Babeldaob possible. The majority of the country's population resides on the island of Koror but many have plans to build and resettle on Babeldaob after the road is completed. Others have plans to lease land to foreign developers for building vacation homes for Asian tourists, building resorts and some even propose building golf courses. The impact of such development on such a tiny island ecosystem will be severe.

Invasive species are playing an increasingly significant role in Palau though this has not to date been as extreme as has happened on other Pacific islands such as Hawaii. Much on this topic has been treated elsewhere. Notable invasive plants include the interestingly native but invasive vine *Merremia peltata, Clidemia hirta* in the understory, and *Falcataria moluccana, which* towers over the native canopy layer out-competing native trees. On a whole however, invasive species appear to be a secondary or lesser threat to that of habitat loss. Areas of Babeldaob harboring major invasions of non-native plants tend to be previously disturbed areas. The primary forest remains very much intact and native. From the pollen record, Athens & Ward (2002) documented that Palau's native forests displayed resilience to introduced species brought by early Palauans, giving the island a "non-insular" character. This curious documentation is worthy of further investigation.

Climate change has been documented as a significant threat to existing rare plant populations across the globe (Harte et al. 2004; Thomas et al. 2004; Hannah et al. 2005;). Modeling techniques have been developed that can predict the amount of change that particular ecosystems are expected to undergo given current global warming trends (Li & Hilbert 2008; Beaumont et al. 2005, 2008; Hijmans & Graham 2006). Whilst modeling methods are still developing, it is well established that native ranges of many plant species are expected to change significantly as global temperatures rise and rainfall patterns change (Bartlein et al. 1997; Matsui et al. 2008; Tylianakis et al. 2008; Wirth et al. 2008). This can, and is likely to, lead to many extinctions where species' ranges are restricted. Habitat fragmentation, which is occurring everywhere on earth at alarming rates, is magnifying this problem presenting additional barriers to plant and animal migration corridors. As a whole, knowledge on this topic is very limited for the tropics (Stork et al. 2007; Colwell et al. 2008). However analyses have been conducted for the Queensland Wet Tropics (Hilbert et al. 2001; Williams et al. 2003), and in other montane areas of the tropics (Colwell et al. 2008; Raxworthy et al. 2008), which stress a significant proportion of species that will be pushed to extinction as their habitable ranges shrink, or even vanish completely leaving them with nowhere to migrate to. Virtually no comparable studies have been conducted for tropical Pacific Islands. However, both the Queensland wet tropics and the montane tropics are comparable to that of Micronesia. Both mountaintops and islands serve to isolate gene pools, which can promote speciation events, but are particularly vulnerable to extinction. The Queensland Wet Tropics region has also been regarded as having an insular character, being a rainforest pocket within an arid continent. It also shares many genera with Palau. Given this, it is reasonable to expect similar future climate change induced species extinctions on islands of the Pacific. Further information and study on this issue is urgently needed, as vegetation turnover in response to past climate change in the Pacific palaeoenvironmental record is a hotly debated topic.

This evidence presented above justifies the application of IUCN red list criteria B (b(iii)) for several of Palau’s endemic plants. This criterion refers to a continuing decline in area/extent or quality of habitat. Clearly Palau’s forests as a whole have been in decline since early human occupation. There has likely been some regeneration at particular intervals, but the current trend with the opening of Babeldaob for development is certainly continuing decline. Since very few population-based studies have been conducted in Palau, this criterion, in addition to cases where species qualify as fragmented and very small in population size, have been the primary criteria used for establishing threatened status in this report. It is hoped that a comprehensive study can be funded and conducted to assess all of Palau’s endemic plants. This will not only improve the data presented here by conducting population studies but also fill the huge data deficiency gap for Palau’s poorly known taxa. Although the rate of data deficiency for Palau is exceptionally high, this is not surprising. In one of their recent global assessments, the IUCN (Baillie et al. 2004) determined that only 4% of the worlds described plant species have been evaluated under the IUCN Red List Criteria (IUCN 2001). Since 3% of these are listed as threatened it is evident that assessments have been biased towards selected taxa that are known to be threatened. Considering the known threats, and the vulnerability of island endemics to extinction, it is imperative that Palau’s 61% data deficient endemic plants are assessed. If a threatened species does not have formal recognition of its rarity, it is very difficult to justify its protection and prevent the loss of crucial habitat. In 2001, the Conservation International established a goal to increase the number of plants on the IUCN Red List to meet the 2010 CBD target of obtaining preliminary assessments of all the world’s described plant species (Baillie et al. 2004). Since Palau is a member of the CBD this need is even more relevant. Focusing efforts of the assessment first on the endemics is an obvious priority. This has been successfully achieved in much larger tropical regions including the island of Socotra, Ecuador (Baillie et al. 2004) and is a realistic goal for Palau.

CONCLUSION

A total of 130 endemic plants are listed here as endemic to the Palau archipelago, 75 restricted to volcanic islands, 31 restricted to limestone, and 24 occurring widespread. Several of these are known to have small, restricted ranges and a total of 7 qualify for threatened status under the IUCN red list criteria. Although there is a considerable paucity of data for over half of Palau's endemic plants it can be expected that at least 15% are threatened. It is clear that the plants with restricted ranges on the volcanic islands are the most threatened due to human activities, primarily forest clearance. Evidence suggests that this is not a recent trend but has continued from the very first early Palauan settlers. Recent development however has accelerated this trend significantly making the need for a complete understanding of the distribution of Palau's endemic plants more pertinent then ever. A full scale IUCN red list assessment for all of Palau's endemic plants, especially those listed as data deficient in this paper, is urgently needed along with studies investigating the degree of threat posed by climate change.

The results presented here are by no means a final product. It is expected that the number of endemic species cited here will actually decrease as further taxonomic studies are conducted, not increase as has been previously suggested. The discovery of a few new species is also likely. However the likelihood of several species listed here as endemic being reduced to synonymy in the future is much higher. Furthermore, as additional collections are made and studies are conducted, current understandings of plant distributions may change.

ACKNOWLEDGEMENTS

This paper was many years in the making and would not have been possible without the help and support of innumerable people and several institutions, which cannot all be listed here. We thank the Republic of Palau, the Belau National Museum, UNESCO, The Nature Conservancy, Peace Corps, The Royal Botanic Gardens Edinburgh, the University of Adelaide, Kew Gardens, the Bishop Museum, USDA

Natural Resources Conservation Service, and the National Tropical Botanic Garden, and the Smithsonian Institution. Our personal gratitude also extends in no particular order to Tarita Holm, Naito Soaladaob, Julian Dendy, Andy Lowe, Louise Ronse de Craene, David Lorence, Michael Balick, Tony Miller, Robert Gavenda, Agnes Rinehart and Gunnar Keppel.

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CHECKLIST OF ENDEMIC SPECIES

Taxon name - Substrate - Form – Abundance – Status

Lycophyta
SELLAGINELLACEAE
Selaginella dorsicola Hosok. V H U DD
Selaginella palauensis Hosok. V H U DD
Selaginella pseudo-volkensii Hosok. V H U DD

Pteridophyta
LOMARIOPSIDACEAE
Cyclopeltis kingii (Hance) Hosok. L H-E DD DD
PTERIDACEAE
Adiantum palaoense C. Chr. * V H DD DD
Pteris tapeinidiifolia H. Itô * L H-E DD DD
POLYPODIACEAE
Grammitis palauensis Hosok. + V E DD DD
Prosaptia palauensis Hosok. V H DD DD
THELYPTERIDACEAE
Thelypteris carolinensis (Hosok.) Fosberg + L H DD DD
Thelypteris pseudarfakiana (Hosok.) C.F. Reed
* V H DD DD
Thelypteris rupi-insularis Fosberg + L H DD DD

Basal Angiosperms
ANNONACEAE
Goniothalamus carolinensis Kaneh. V T U-R NT
Polyalthia merrillii Kaneh. * L T DD DD
MYRISTICACEAE
Horsfieldia palauensis Kaneh. G T C LC
PIPERACEAE
Peperomia kraemeri C.DC. G H DD LC
Peperomia palauensis C.DC. G H C LC
Piper hosokawae Fosberg G L C LC

Monocots
ARECACEAE
Ponapea palauensis Kaneh. L T U-R **CE** (B2abc)
Hydriastele palauensis (Becc.) W.J.Baker &
Loo L T U-R NT
CYPERACEAE
Hypolytrum flavinux (T.Koyama) D.A.
Simpson * V H DD DD
Fimbristylis palauensis Ohwi * V H DD DD
ORCHIDACEAE

Bulbophyllum desmanthum Tuyama * V E DD DD
Bulbophyllum hatusimanum Tuyama V E DD DD
Chiloschista loheri Schltr. G E C LC
Cleisostoma porrigens (Fukuy.) Garay V E U DD
Crepidium calcarea (Schltr.) D. L. Szlachetko L H DD DD
Crepidium kerstingiana (Schltr.) D.L.
Szlachetko * G H U DD
Crepidium palawensis (Schltr.) D. L.
Szlachetko V H U LC
Crepidium setipes (Schltr.) D. L. Szlachetko V H A LC
Cystorchis ogurae (Tuyama) Ormerod &
P.J.Cribb V H DD DD
Dendrobium brachyanthum Schltr. V E C LC
Dendrobium implicatum Fukuy. V E DD DD
Dendrobium kerstingianum Schltr. * V E DD DD
Dendrobium palawense Schltr. * L E DD DD
Dendrobium patentifiliforme Hosok. + V E DD DD
Dipodium freycinetioides Fukuy. V E C DD
Liparis dolichostachya Fukuy. + V H-E DD DD
Liparis palawensis Tuyama * V H-E DD DD
Liparis yamadae (Tuyama) Fosberg & Sachet * V H-E DD DD
Micropera draco (Tuyama) P.J. Cribb & P.
Ormerod + V E DD DD
Moerenhoutia laxa Schltr. V H U DD
Nervilia trichophylla Fukuy. + V H R NT
Oberonia palawensis Schltr. G E-H DD LC
Peristylus palawensis (Tuyama) Tuyama V H R NT
Phreatia kanehirae Fukuy. V E DD DD
Phreatia palawensis (Schltr.) Tuayama L E DD DD
Robiquetia palawensis Tuyama G E DD DD
Taeniophyllum palawense Schltr. V E U DD
Zeuxine palawensis Tuyama V H C LC
PANDANACEAE
Freycinetia villalobosii Martelli V L C-A LC
Pandanus aimiriikensis Martelli V T(u) C-A LC
Pandanus kanehirae Martelli V T U NT
Pandanus lorencei Huynh + L T DD DD
Pandanus macrojeanneretia Martelli V T U DD
Pandanus palawensis Martelli V T DD DD
Pandanus peliliuensis Kaneh. + L T-S DD **VU** (D2)
POACEAE
Panicum palauense Ohwi * V H DD DD

Eudicots
ACANTHACEAE
Hemigraphis palauana Hosok. + V H DD DD

Pseuderanthemum inclusum Hosok. V H DD DD
ANACARDIACEAE
Buchanania palawensis Lauterb. G T C LC
APOCYNACEAE
Melodinus insularis (Markgr.) Fosberg * V L DD DD
Rauvolfia insularis Markgr. V T U,RR **VU** (D1,2)
ARALIACEAE
Osmoxylon oliveri Fosberg & Sachet G T(u) A LC
Osmoxylon pachyphyllum (Kaneh.) Fosberg & Sachet G T(u) U LC
Osmoxylon truncatum (Kaneh.) Fosberg & Sachet + V T(u) DD DD
BORAGINACEAE
Cordia micronesica Kaneh. & Hatus. V T U-R DD
CAPARIDACEAE
Capparis carolinensis Kaneh. * L S DD DD
CELASTRACEAE
Maytenus palauica (Loes.) Fosberg G S C LC
CLUSIACEAE
Calophyllum pelewense P.F. Stevens V T(c) U DD
Garcinia matsudai Kaneh. V T C-A LC
Kayea pacifica Hosok. V T U, DD DD
COMBRETACEAE
Terminalia crassipes Kaneh. & Hatus. V T(c) A, RR **EN** (B1ab(iii) +2a,b(iii))
CUCURBITACEAE
Trichosanthes hosokawae Fosberg * L L DD LC
ELAEOCARPACEAE
Elaeocarpus rubidus Kaneh. + L T DD DD
EUPHORBIACEAE
Claoxylon longiracemosum Hosok. V T U DD
Cleidion sessile Kaneh. & Hatus. L T DD DD
FABACEAE
Crudia cynometroides Hosok. V T U DD
Dalbergia palauensis Hosok. V L DD DD
Parkia parvifoliola Hosok. V T(c) R, RR **EN** (B1ab(iii) +2ab(iii))
GENTIANACEAE
Fagraea ksid Gilg & Benedict V T C LC
GESNARIACEAE
Cyrtandra palawensis Schltr. V L U-C LC
Cyrtandra todaiensis Kaneh. L S DD LC
MALVACEAE
Sterculia palauensis Kaneh. L T(c) DD DD
Trichospermum ledermannii Burret V S A LC
MELESTOMATACEAE
Astronidium palauense (Kanehira) Markgr. V T(u) C LC
Medinilla blumeana Mansf. V L DD DD
MYRSINACEAE
Discocalyx mezii Hosok. * G T(u) U, DD DD

Discocalyx palauensis Hosok. + L T DD DD
Maesa palauensis Mez * L S DD LC
Myrsine palauensis (Mez) Fosberg & Sachet V T(u) C LC
MYRTACEAE
Syzygium palauensis (Kaneh.) Hosok. * G T DD
OLACACEAE
Anacolosa glochidiiformis Kaneh. & Hatus. G T U DD
PHYLLANTHACEAE
Cleistanthus carolinianus Jabl. G T U LC
Cleistanthus insularis Kaneh. * V T U DD
Glochidion macrosepalum Hosok. G S DD LC
Glochidion palauense Hosok. * G T C LC
Phyllanthus palauensis Hosok. V S C-A LC
Phyllanthus rupi-insularis Hosok. L S DD LC
PUTRANJIVACEAE
Drypetes nitida Kaneh. G T C LC
RHAMNACEAE
Ventilago nisidai Kaneh. V L-S DD DD
RUBIACEAE
Badusa palauensis Valeton G T C LC
Bikkia palauensis Valeton L S C LC
Hedyotis aimiriikensis Kaneh. * V S DD DD
Hedyotis cornifolia Kaneh. V H DD DD
Hedyotis korrorensis (Valeton) Hosok V S C-A LC
Hedyotis sachetiana Fosberg * V S DD DD
Hedyotis suborthogona Hosok. + V H DD DD
Hedyotis tomentosa (Valeton) Hosok. G H C DD
Hedyotis tuyamae Hosok. V S DD DD
Maesa canfieldiae Fosberg & Sachet * L T-S DD **VU** (D2)
Morinda latibractea Valeton L T(u) U DD
Morinda pedunculata Valeton V S-T C LC
Ophiorrhiza palauensis Valeton G H U DD
Psychotria cheathamiana Kaneh. * L T(u) DD DD
Psychotria diospyrifolia Kaneh. V L-S U DD
Psychotria mycetoides Valeton + V S DD DD
Timonius corymbosus Valeton G T-S DD DD
Timonius korrensis Kaneh. + L T DD DD
Timonius mollis Valeton V T(u) DD DD
Timonius subauritus Valeton V S C LC
Timonius salsedoi Fosberg & Sachet + V T(u) DD **CE** (B1ab(iii) +2,ab(iii))
RUTACEAE
Melicope palawensis (Lauterb.) T.G.Hartley L S C LC
Melicope trichantha (Lauterb.) T.G.Hartley * V S-T DD DD
SAPINDACEAE
Elattostachys palauensis Hosok. + L T DD DD
SAPOTACEAE

Manilkara udoido Kaneh. V T C-D,RR LC
Planchonella calcarea (Hosok.) P. Royen L T DD DD
SALICACEAE
Casearia hirtella Hosok. G T C LC
URTICACEAE
Elatostema stoloniforme Kaneh. * V H DD DD
Pipturus micronesicus Kaneh. * L S DD DD
VITACEAE
Cayratia palauana (Hosok.) Suesseng. + L L DD DD

Checklist of Endemic Varieties

Taxon name – Substrate – Form – Abundance

ARECACEAE
Heterospathe elata Scheff. var. *palauensis* (Becc.) Becc. G T C-D
CLUSIACEAE
Calophyllum inophyllum var. *wakamatsui* (Kaneh.)
Fosberg & Sachet V T A
Garcinia rumiyo var. calcicola Fosberg L T C
EBENACEAE
Diospyros ferrea (Willd.) Bakh. *var. Palauensis* (Kanehira) Fosberg G T(u) C
EUPHORBIACEAE
Acalypha amentacea Roxb. *var. heterotricha* Fosberg * V S C
Acalypha amentacea Roxb. *var. palauensis* Fosberg + L S R
FABACEAE
Serianthes kanehirae var. *kanehirae* Fosberg G T U-C
GENTIANACEAE
Fagraea berteroana var. *galilai* (Gilg & Benedict) Fosberg V HP U
ORCHIDACEAE
Zeuxine palawensis var. variegata Tuyama * V H U
PIPERACEAE
Peperomia palauensis C.DC. var. *occidentalis* Fosberg L H U-C
POACEAE
Pschaemum polystachyum Presl var. *chordatum* (Trin.) Fosberg &Sachet V H DD
Paspalum orbiculare G. Forst. var. *otobedii* Fosberg & Sachet V H DD
RUBIACEAE
Hedyotis divaricata (Valeton) Hosok. var. *divaricata* V H R
Psychotria hombroniana var. *canfieldiae* Fosberg L T(u) C
Psychotria hombroniana var. *peliliuensis* Fosberg + L T(u) DD
Psychotria rotensis var. palauensis (Hosok.) Fosberg L T(u) C
Timonius corymbosus Valeton *var. takamatsui* Fosberg & Sachet L S DD
Timonius mollis Valeton *var. submollis* Fosberg & Sachet V T(u) DD
Timonius mollis var. villosissimus (Kaneh.) Fosberg & Sachet V S DD
Timonius subauritus var. strigosus Fosberg & Sachet V S DD
Uncaria lanosa var. korrensis (Kaneh.) Ridsdale V S C

SCROPHULARIACEAE
Limnophila fragrans (G. Forst) Seem var. *brevis* Schltr. ? H DD
SYMPLOCACEAE
Symplocos racemosa Roxb. *var. palauensis* (Koidz.) Nooteb. V T A

CHAPTER 2

Using the ancient past for establishing current threat in poorly inventoried regions

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Biological Conservation 147 (2012): 153-162

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ABSTRACT

The need for a global priority list for threatened plants has been widely recognized by the conservation community, yet the threatened status of the majority of the world's plants species remains poorly known. This is especially true in the tropics and the oceanic islands of the Pacific, where progress towards the targets of the Global Strategy for Plant Conservation (GSPC) 2011-2020 is hindered by the paucity of complete species distribution data. Here we outline a new methodology to undertake threatened species assessments where detailed contemporary population data is lacking. This new interdisciplinary methodology draws upon the synthesis of archaeological and botanical data to calculate a percentage of long-term decline in habitat quality. We use this method to assess the threatened status of the endemic flora of Palau, Micronesia, a Pacific island nation known for its high levels of plant diversity and endemism, by utilizing data extending back to human colonization of the archipelago. For Palau, we calculate the percentage of a long-term decline in habitat quality to be 31-39% of the total available range of 55% of the endemic plant species. These data are also used to address a long debated question in the western Pacific: Are the origins of the savanna vegetation anthropogenic? Strong evidence for anthropogenic savannas in Micronesia support the estimated extent of historic deforestation in Palau. This new method worked well in our case study, and can be used in other locations with incomplete species distribution data to establish a first basis for conservation prioritization.

Key words: threatened species, red list, environmental archaeology, savanna, anthropogenic

1. INTRODUCTION

In 2002 the Convention on Biological Diversity (CBD) adopted a Global Strategy for Plant Conservation (GSPC), which targeted a preliminary assessment of the conservation status of all known plant species by 2010 (Baillie et al. 2004). To date in Oceania, excluding Australia, New Zealand and Hawai'i, there have been a total of 1,304 IUCN red list assessments completed (IUCN 2010) which have been estimated to comprise approximately 9% of the total known and described plant diversity in the Pacific islands region (Pippard 2008). Up to date data on the total number of indigenous plant species from the major Pacific islands and archipelago regions suggests this estimate is over-estimated by approximately 6% (Table 1). Of all the regions where accurate data is available, only 3% out of the total number of species have been assessed with IUCN Criteria to date suggesting that at least 95% of the plant species native to underdeveloped countries of the Pacific Island bioregion await IUCN threat assessment.

The CBD reconvened in 2010 to revise the original targets and extended the GSPC targets to 2020. New targets include aims for "an assessment of the conservation status of all known plant species, as far as possible, to guide conservation action" (Secretariat of the Convention on Biological Diversity 2011). Although the more developed nations of Oceania, including Australia, New Zealand, and the US state of Hawai'i all have independent legislation for assigning and monitoring threatened status of species, the IUCN Criteria are still widely promoted as both a global standard for assessing threat and for application in regions where national legislation is lacking. In this study we argue strongly that in order to even approach the ambitious GSPC 2020 target, alternative methods of assessing threatened status of plant species are absolutely necessary. Here we present one such alternative method, which is specifically designed for application in poorly inventoried floras such as Oceania. Our method is outlined in seven steps using a case study from Palau, Micronesia.

Table 1. Percent of the native flora assessed under IUCN Criteria for respective regions of Oceania (See Supplementary Data 1 for complete list of data sources).

Region	Native Plants (Vascular)	% Endemism of Native Flora	IUCN Plant Assessments	% of Native Flora Assessed
New Guinea	25 000+	~ 90%	317	1%
Norfolk Island	136	32%	3	2%
Samoa	550	30%	20	4%
Tonga	340	4%	16	5%
Solomon Islands	1,941	unknown	88	5%
Vanuatu	870	~ 15%	46	5%
Micronesia	1,227	30%	97	8%
Fiji	1,594	54%	141	9%
New Caledonia	3,137	79%	346	11%
Total	**34 795**	**---**	**1074**	**3%**

Considering the vulnerability of islands to biological extinctions, the lack of red list assessments to date in the Pacific is of concern. Of the world's recorded extinctions for mammals, birds, amphibians, reptiles and mollusks, 72% were island species (Baillie et al. 2004) suggesting that the Polynesia-Micronesia Biodiversity Hotspot (Myers et al. 2000), though not as rich in species as many other global biodiversity hotspots, is potentially more vulnerable to extinctions. It is probable that the loss of many species of Oceania's flora and fauna have gone unrecognized and unrecorded. Many studies have indicated that entire assemblages of species became extinct following the colonization of the Pacific by early humans. Extinctions associated with early settlement of the Pacific have been well documented in the palaeorecord for plants (Prebble and Dowe 2007), birds (Holdaway 1989; Athens et al. 2002; Steadman 2006), amphibians (Holdaway 1989), reptiles (Pregill and Steadman 2004) and insects (Porch 2007; Porch et al. 2007).

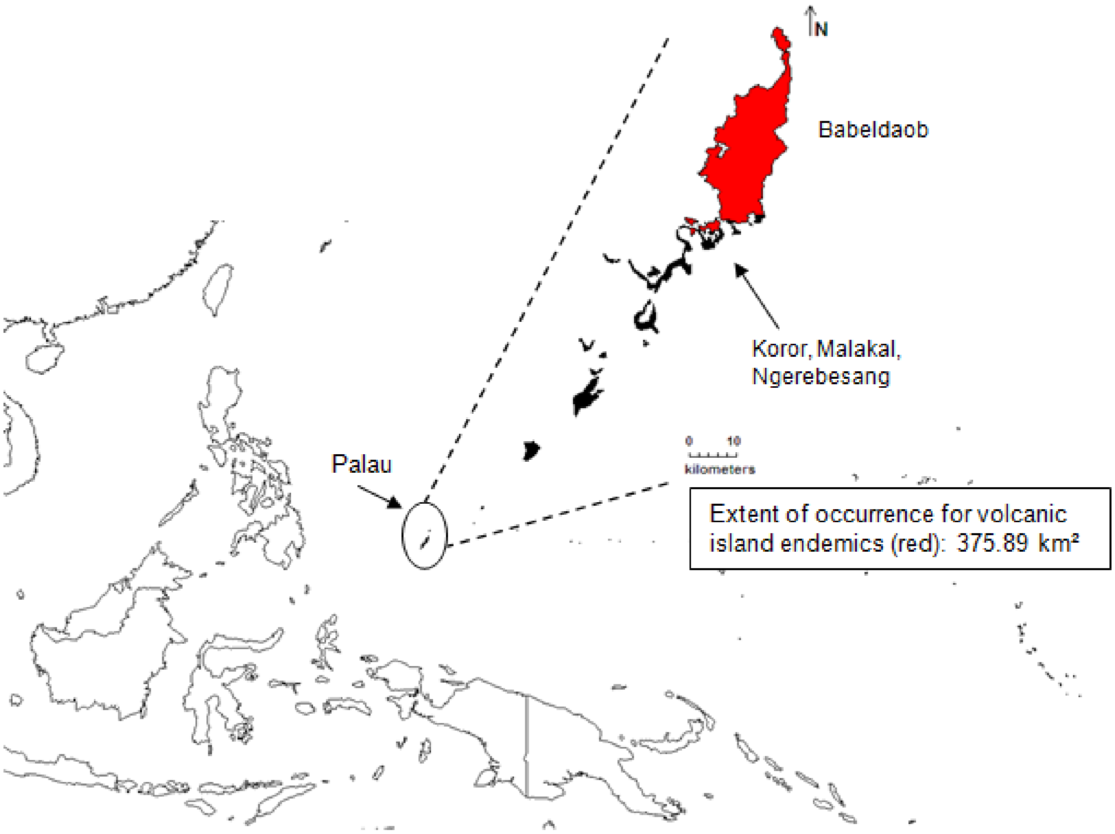
Despite this wealth of palaeoenvironmental and archaeological data, current IUCN Criteria only enable assessments to draw from evidence extending ten years or three generations into the past. Here we argue that in the Pacific, and likely other poorly known tropical regions, the palaeoenvironmental and archaeological record is often the best evidence available for identifying population declines of poorly known species. Failure to utilize and draw inferences from these disciplines to inform conservation policy will only ensure the continued slow progress towards threat assessment and in some cases may come too late to help save species from extinction. To test out this new methodology, the Pacific island nation of Palau is used as a case study, where evidence for an anthropogenic origin of a contended vegetation type revealed measurable declines in the populations its endemic plant species.

1.1 Background – Palau overview

Palau is an archipelago of more than 350 islands extending 150 km along a north to southwest-trending arc in the western Caroline Islands approximately 900 km north of West Papua and 870 km east of the Philippines at the western limit of the Polynesia-Micronesia Biodiversity Hotspot. Palau has tropical broad-leaved evergreen moist forest occurring on several larger volcanic islands, and numerous atoll, platform-like, and uplifted karst limestone islands. The archipelago is regarded for having the most diverse flora of all the Micronesian islands in both number of native and endemic plant species. This study focuses on the 75 plant species restricted to Palau's 375.89 km^2 of volcanic islands (Figure 1) and draws upon evidence from Palau's palaeoenvironmental, archaeological and historical records to quantify an inferred past decline in native forest habitat.

A preliminary IUCN red list assessment of Palau's endemic plants was conducted (Costion et al. 2009), however detailed distribution data was lacking for 61% of the species, and were categorized as "DD" (Data Deficient). Here we re-assess the Palau endemic flora with our new proposed methodology that enables a complete assessment with the existing available data.

Figure 1: Geographical range and total area of occupancy of the taxa under assessment



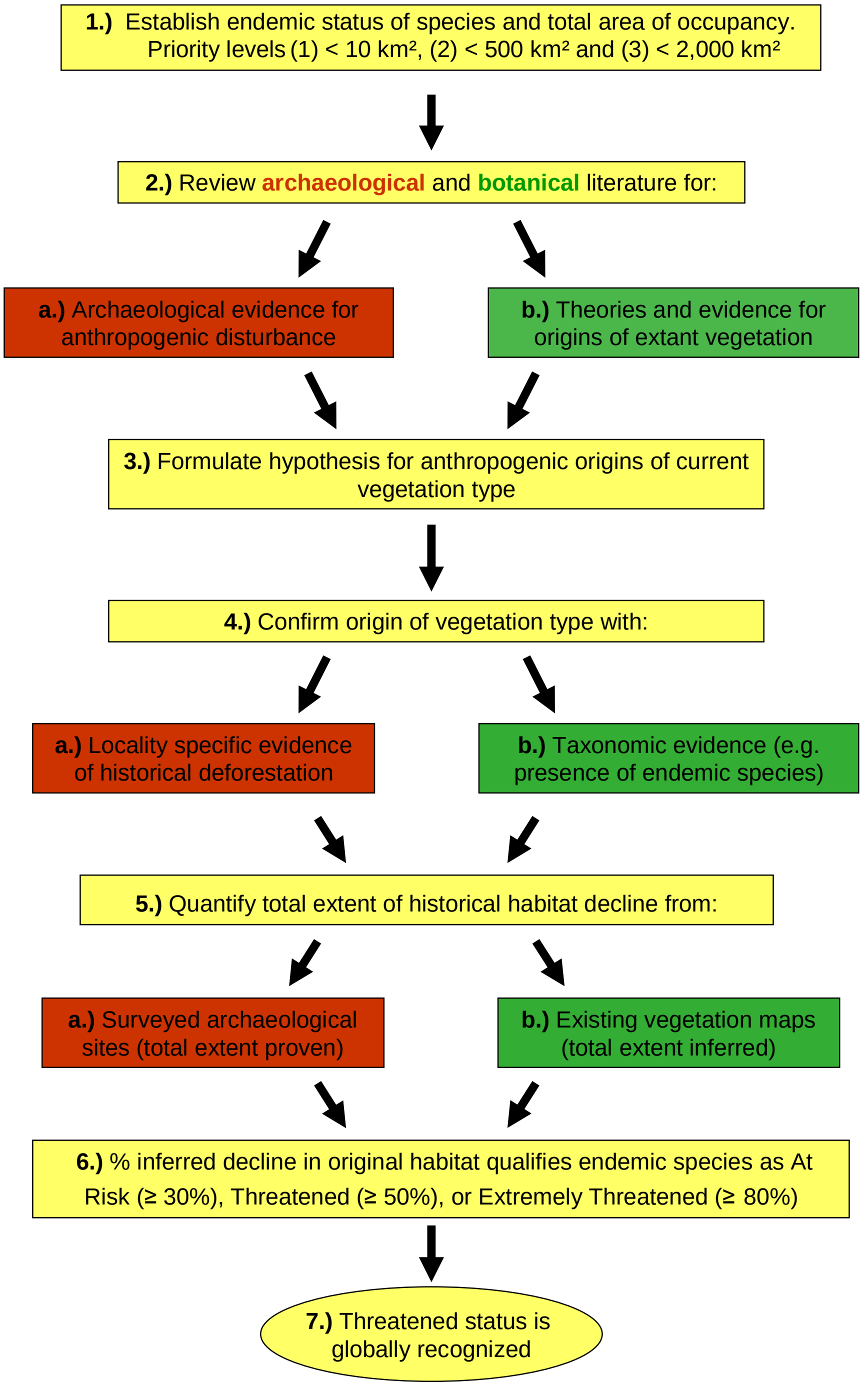
Substantial deforestation is identified in Palau's palaeorecord by an increase in savanna indicators along with a rise in the frequency of microscopic charcoal particles between about 4400/3000 and 3800/2500 cal BP (Athens and Ward 2002, 2005; Athens and Stevenson 2010) and in the form of remnant terrace formations (Figure 2) derived from earthwork construction and use that began over 2000 years ago (Liston 2007, 2009). During Palau's Japanese era (1914-1944), Babeldaob's land-cover also experienced significant and widespread human-induced impact (Iida 2011) from the production of cash crops, harvesting of timber, and strip-mining. These anthropogenic activities, which would have stripped the forest bare, provide dated evidence for forest succession studies (Liston et al. 2011). Although the cause of transition from forest habitat to savanna in Micronesia has remained a hotly debated topic, here we provide new evidence to support an anthropogenic origin of Palau's savanna. Our demonstrated utilization of this evidence of long term decline in habitat quality for threatened species assessments has substantial implications for progressing biodiversity conservation at local, regional and global scales.

Figure 2: Aerial photograph of part of Ngaremlengui Earthwork District (USGS aerial photo 4_46_2_244 – 1976)

2. METHODS

IUCN Criterion A is based on reductions of species populations that can be observed, estimated, inferred or suspected in the past or future however, these population declines must be measured in periods of ten years or three generations (IUCN 2001). In an attempt to address the serious data deficiency gaps in the IUCN red list, we remove the limitation imposed by the 10 year/3 generation measurable period of decline. This enables archaeological and palaeobotanical evidence to be incorporated into an assessment which are data with the potential to identify historical declines and/or fluctuations in habitat quality coinciding with human activities that can directly indicate measurable changes in extant populations of endemic species. Our methodology has the following seven-step protocol (Figure 3).

Figure 3: Outline of proposed interdisciplinary species assessment methodology



1) Quantify area of occupancy based on plant species endemic status and habitat restrictions (Costion et al. 2009). Loss or fluctuation of habitat within this area can then be

directly attributed to population declines of the endemic species. All plants classified as endemic to volcanic substrates are considered. Following IUCN Criterion B2 we define three categories of area occupancy: 1) < 10 km², 2) < 500 km² and 3) < 2,000 km². Taxa placed in each category can then be weighted or prioritized in numerical order relative to their total population size. This enables prioritization to be assigned to taxa with extremely small natural ranges or areas of occupancy. All taxa in the present study are restricted to an area of occupancy of 375.89 km² (Figure 1) thus receive priority level (2).

2) Conduct a thorough review of the islands' archaeological and botanical literature including documentation of the pollen record, archaeological investigations and detailed species composition of vegetation types. This allows for determination of the likely extent of forest habitat on the archipelago prior to colonization and established evidence of landscape changes that coincided with the initial stages of human settlement (see Athens and Ward 2005).

3) Formulate or build upon an existing or contended hypothesis on the anthropogenic origins vegetation type/s by synthesizing data from multiple disciplines. In the case of Micronesia - savanna.

4) Test of hypothesis to confirm the anthropogenic origin of specific vegetation type/s. For Palau this involved: 1) archaeological and historical evidence of deforestation (See 3.4.1), which included a review of literature and cartographic documents, fieldwork and remote sensing methods relying on historic vegetation maps and aerial photography (see Supplementary Data 2), and; 2) taxonomic evidence for the antiquity of the vegetation type. We define taxonomic evidence (See 3.4.2) as the absence of valid endemic plant species restricted to savanna vegetation. The endemic status of plants allegedly endemic to the savannas of Micronesia was assessed by examining their distribution records and relevant taxonomic literature.

5) Quantify the extent of past identifiable habitat decline and relate it to current land cover by 1) calculating the area of demonstrable anthropogenic disturbance and; 2) overlaying the data onto existing vegetation maps. To accurately reflect the complexity of

Babeldaob's landscape history, we reviewed documented evidence of forest re-growth and recovery in areas where forest habitat loss was directly verifiable. The extent of current intact and disturbed volcanic island habitats was classified (see Supplementary Data 6) using data from Palau's 1976 aerial photograph-based vegetation survey (Cole et al. 1987).

6) Total inferred decline in habitat is used to qualify species restricted to the habitat of assessment as threatened where a ≥30% decline in habitat = At Risk, ≥50% = Threatened with Extinction, and ≥80% = Extremely Threatened. We further define these categories as follows:

> *At Risk*: Species are at risk of extinction and require legislative protection of representative populations and regular monitoring at appropriate intervals to report on their stability.
>
> *Threatened:* Species are under a threat of extinction significant enough to warrant conservation actions and plans to mitigate and revert the ongoing decline.
>
> *Extremely Threatened:* Species require immediate actions and intervention to avert extinction threat.

7) Finally, we discuss how landscape or land-use history can influence interpretations of current vegetation types and the implications that this has for species-based conservation policy. We propose that species from hotspot or tropical regions assessed using the above methodology qualify for globally recognized threatened status.

3. RESULTS & DISCUSSION

Our results are presented following the seven-step methodology.

3.1 Establishing endemic status and habitat restrictions

The most important step in the assessment process, and a high priority in the Pacific, is an up-to-date checklist of endemic species for the flora being assessed that is consistent with current taxonomy and published in a peer reviewed journal. Unpublished lists and/or inferred endemic concepts can lead to the misapplication of conservation policy and funds to widespread species with a variation in, or invalid, species names. The crucial role a current checklist plays in the threatened species assessment is exemplified by the 36% reduction in endemic status of Micronesian plant species from previous estimations made prior to a systematic treatment for the region (Costion and Lorence 2011). The quality of the species assessment utilizing the approach proposed in this study will ultimately rest on the accuracy of applied endemic concepts. Often as in this case, these endemic species distributions can be further defined by known substrate restrictions of particular taxa (Costion et al. 2009).

3.2 Review of archaeological and botanical literature on savanna origins

Botanists have long proposed that the extent of savanna vegetation on Micronesia's islands was restricted before colonization and expanded due to human activities (Merrill 1912; Fosberg 1960, 1962; Barrau 1961). Under this scenario, pockets of grassland were confined to the fresh volcanic slopes in the Northern Marianas and potentially poorly drained soils in other localities. Settlement of these largely forested islands was accompanied by burning of the native vegetation to clear land for agriculture (Barrau 1961), habitation, and line of sight, and to encourage grass growth for thatching material (Kirch 1982), among other activities. An anthropogenic cause for Micronesia's savannas has substantial scientific support largely due to the palaeoenvironmental coring work of

Athens and colleagues (Athens and Ward 2004, 2005; Athens et al. 2004; Athens and Stevenson 2010).

Other researchers disagree and point out the substantial room for misinterpretation of the palaeoenvironmental data (Spriggs and Anderson 1993; Anderson 1994) or provide natural causal mechanisms for savanna expansion (Zan and Hunter-Anderson 1987; Hunter-Anderson 2009). The latter authors present an alternative geoclimatic model, arguing that Pacific island savannas developed by natural means during the drier climate of the Pleistocene and fluctuated in size throughout the Holocene due to climate changes, edaphic conditions and natural fires. We summarize our complete review (Supplementary Data 3) below:

The anthropogenic model

~ There is substantial palynological evidence for a correlation between an increase in savanna indicator species and human colonization of the islands. Prior to human colonization these indicators are minimal or entirely absent from pollen profiles.

~ Several unknown pollen types recorded in Palau’s palaeocores from pre-human times rapidly decrease, some disappear entirely, after human colonization. Similar findings are recorded on other Pacific islands.

~ As the savanna indicators, replicated in multiple cores from widely scattered locations throughout Palau and the Pacific, do not occur simultaneously (Table S1), decline in native forest is interpreted to result from an intense level of human activity rather than being due to a natural phenomenon such as climate change.

~ Archaeological evidence found in savanna covered monumental earthwork complexes (Figure 4) suggests an anthropogenic origin of the vegetation type (See 3.4.1 and 3.5.1).

Figure 4: Step-terace complex in the Ngaremlengui Earthwork District (Photo by J. Liston)

The geoclimatic model

~ The presence of charcoal in the fossil record long before possible human colonization suggests natural occurrence of fires. However this argument is taken out of context from the relative amount and size of the particles occurring prior to colonization. Microscopic charcoal can be in record before people arrived due to atmospheric transport but is much smaller in size than the charcoal particles associated with local human activity. Further more Athens and Ward (2005) demonstrated that charcoal and naturally occurring lignite cannot be distinguished in palynological sequences.

~ Soil conditions are suggested to have had a contribution to the natural occurrence of savannas however there is no geological or edaphic evidence to support this claim in Palau.

~ Climate change particularly the El Niño/Southern Oscillation (ENSO) weather system is invoked to account for a natural origin of savannas. This claim is drawn from trends observed in other distant bioregions and lacks any evidence for a correlation in timing of the onset of change between the two bioregions nor a correlation between recorded changes in climate and increase of savanna indicators in pollen profiles.

~ The existence of plants that are allegedly endemic to the savanna vegetation are considered proof for the natural origin of savannas. However taxonomic review of these species indicates that these species naturally occur in other native habitats and are not restricted to savannas in Micronesia (See 3.4.2).

3.3 Hypothesis – Palau's savannas are anthropogenic

Concurring with previous authorities (Fosberg 1998; Manner et al.1999; Athens and Ward 2004), we hypothesize that Palau's savanna vegetation is all or nearly all anthropogenic, with pre-human occupation extent being minimal. The immediate implication of this hypothesis is that quantification of the savanna vegetation will provide a minimum total extent of habitat decline since human colonization. If our hypothesis is correct then there should be substantial evidence for ancient and historic large-scale deforestation. We should also expect to find few if any endemic plants restricted to savanna habitat due to the recent origin savannas in Micronesia on the evolutionary timescale. Although the alleged existence of savanna endemics has been discussed previously, this is the first time the issue is addressed with a systematic review of the taxonomic evidence.

3.4.1 Locality specific archaeological and historical evidence of disturbance

Clearing of Babeldaob's forest likely began at colonization (between 4300-3200 cal BP). Most of the very early impacts to land-cover are not detectable in the archaeological record or quantifiable in the palaeorecord. However, construction of often massive earthwork complexes from c. 2400-1200 cal BP followed by the formation of more modest step-terraces that continued until several hundred years ago left an indelible mark on the landscape (Liston 2007, 2009). A significant amount of ancient terracing has been identified and mapped by a combination of pedestrian field survey and remote sensing methods (Liston 2011) providing spatial proof for areas that have undergone habitat decline in the past.

Babeldaob's transformation into an agricultural and industrial landscape during the Japanese era (1914-1944) also resulted in widespread deforestation (Iida 2011). The Nanyo-Cho (South Seas Government) located its capital on Koror in 1922 and Palau became the primary agricultural production center for Japan's Micronesian colonies with plantations producing enough cash crops for export to Japan and forestry operations exploiting local timber from forests for firewood and charcoal. Bauxite strip-mining operations from 1940 to 1944 yielded 369 227 tons of bauxite ore, (Miyaoka 2010) meeting nearly 10% of Japan's aluminum consumption (Bridge and Goldish 1948). With Japanese vegetation survey maps and World War II era aerial photographs, a percentage of these activities were identified and quantified from plantations, settlements, military training grounds and other sizeable enterprises (Liston et. al. 2011).

3.4.2 Taxonomic evidence - Micronesia's savanna endemics

Previous inferences that the occurrence of endemic plant species in Micronesia's savannas is evidence of naturally occurring ancient savannas were based on poorly understood and confused taxonomic regional boundaries and also lacked evidence from field inventory of the candidate species. The vast majority of Micronesia's endemic plant species, 364 (Costion & Lorence 2011), are restricted to forest habitat with comparatively few endemics (Table 2) potentially constrained to the savannas (see Supplementary Data 4 for detailed review).

Our review of Palau's potential savanna endemics suggests that they all can be placed in at least one of two categories: 1) species occurring both in savanna and other sun-exposed native habitats, and 2) species with insufficient taxonomic support for use in scientific hypotheses. Extensive vegetation surveys conducted on Babeldaob identified a high correlation in species composition between savanna-forest edges and upland ridgeline forests (Costion and Kitalong 2006). This association, confirmed by a vegetation cluster analysis performed using Two-Way Indicator Species Analysis (Costion 2007), was attributed to the comparable levels of sun exposure or canopy closure between the two habitats. Other savanna associates not found along upland ridgeline forests are known to occur on exposed basalt outcrops receiving full sunlight.

Existing data on the taxonomy and distribution of savanna taxa suggest that prior to human settlement, savanna vegetation was possibly associated with outcrops or the volcanic slopes of the Mariana Islands from which they later dispersed to areas cleared of forest by humans. Ample records of Micronesian “savanna endemic” plants occurring in sun-exposed habitats other than savanna directly refute the argument that shade intolerant plants are evidence of the antiquity of savannas (Hunter-Anderson 2009).

Advocates of the conflicting hypotheses agree that savanna lands originated during the Pleistocene, very recently from an evolutionary perspective. Although Palau is geologically dated to approximately 30-37 million years old, the onset of climate change in the Pleistocene would not have allowed sufficient time for a diverse radiation of species to take place. Ultimately, if Palau’s savanna vegetation had any relictual character then it should persist without human intervention. Studies have shown the contrary, that when savanna areas are left alone and not subjected to intentional burning, the adjacent forest expands to reclaim the savanna (Supplementary Data 5).

Table 2. Candidate "savanna endemics" of Micronesia.

Family	Species	Endemic to	Notes
MALVACEAE	*Trichospermum ledermannii*	Palau	Common in disturbed areas and savannas, likely also occurs on exposed rock outcrops
MYRTACEAE	*Myrtella bennigseniana*	Micronesia	Shrub occurring in savanna and disturbed areas
PHYLLANTHACEAE	*Phyllanthus palauensis*	Palau	Shrub, not confined to savanna, also occurs on exposed volcanic rock outcrops
	Phyllanthus saffordii	Marianas	Shrub occurring in savanna
	Glochidion marinanum	Micronesia	Shrub occurring in savanna and on limestone
POACEAE	*Ischaemum longisetum*	Marianas	Herb occurring in limestone coastal areas and savanna
	Panicum palauense	Palau	Grass occurring in savanna, very poorly known and studied
RUBIACEAE	*Hedyotis aimiriikensis*	Palau	Likely a synonym with *H. korrorensis*, only known from type collection
	Hedyotis korrorensis	Palau	Shrub, not confined to savannas, also occurring on exposed volcanic rock outcrops
	Hedyotis laciniata	N. Marianas	Shrub confined to Northern Marianas volcanoes in open savanna
	Hedyotis sachetiana	Palau	Doubtful species, known only from type which lacks flowers. Likely synonym of *H. tomentosa*
	Hedyotis suborthogona	Palau	Potentially synonym with *H. fruticulosa*. Only known from two collections.
	Hedyotis tomentosa	Palau	Small shrub, common in savanna but also known from other exposed, and eroded habitats.
	Morinda pedunculata	Palau	Shrub common in open savanna, also occurring along savanna edge and along forested ridges.
	Timonius albus	Yap	Shrub or small tree; extent of occurrence unknown
	Timonius subauritus	Palau	Shrub common in open savanna, also occurring along savanna edge and along forested ridges.

3.5.1 Total extent of habitat decline proven – Historical evidence

Evidence for historic terrace complexes occurs on 45.5 km^2 (14.2%) of Babeldaob's volcanic landscape with an estimated minimum of 18 km^2 additional forested sites yet to be mapped (Liston 2011). Therefore at least 63 km^2 (20.1%) of Babeldaob was shaped into earth structures in the past. Of this estimated total, approximately 14 km^2 (22%) of terraced land is currently in savanna vegetation and the remaining 49 km^2 (78%) is forested. These forested earthwork sites are direct evidence of forest regeneration while the savanna sites are evidence of habitat decline without recovery.

Analysis of cartographic data indicates that during the Japanese era, Babeldaob's forest declined by 52 km^2 largely due to agricultural development, strip-mining operations, and military build-up (Iida 2011). Only about 8 km^2 of this historic deforestation occurred on land cleared during ancient earthwork construction (Liston et al. 2011).

Babeldaob's quantifiable change in land-cover from ancient times until 2006 is identified to be about 31% (97.6 km^2) of the island's volcanic terrain (Liston et al. 2011). This calculation increases to at least 37% (115.6 km^2) when the estimated undocumented earthwork sites are considered. At least 55% of Babeldaob's current savanna vegetation coincides with the archaeological and cartographic evidence for human forest clearing directly supporting an anthropogenic origin. When these quantifications are recalculated to exclude Babeldaob's limestone forest and include Palau's other volcanic islands the total of proven habitat decline or fluctuation amounts to 31% of Palau's volcanic island total land area. Many other ancient activities (e.g., swidden cultivation) that required extensive land clearance left behind little archaeological surface evidence in Babeldaob's transforming landscape. Hence, the extent of original forest habitat decline should be substantially more than the archaeologically quantifiable (Liston et al. 2011).

3.5.2 Total extent of habitat decline inferred – The current vegetation

Intact habitat on Palau's volcanic islands totals to c. 278 km^2 (74%) and disturbed habitat equals c. 98 km^2 (26%) (Supporting Information 6). Adding proven land-use history data (3.5.1), the area of disturbed habitat increases to 147 km^2 (39%), when re-forested earthworks (49 km^2) are subtracted from the 'intact habitats' category. This provides a more accurate quantification of current vegetation impacted by human activities in the past, accounting for possible biodiversity losses that may have occurred when the forest was originally cleared. The inferred total allows for an informed application of the precautionary principle considering extinction trends recorded for other islands throughout the Pacific. A minimum of 13% of forest habitat fluctuation, where original forest was cleared then subsequently reforested, is directly quantifiable. As Palau's savanna-forest edges are known to respond dynamically to the fires routinely ignited by humans the actual fluctuation is likely much higher. Although providing the best estimate to date of disturbed habitat on Palau's volcanic islands (39%), these figures are considered a low estimate of vegetation impacted by human activities.

3.6 Assigning threatened status from inferred habitat decline

The data and studies reviewed have enabled calculation of the minimum extent of human altered habitat, where at least 55% of Palau's extant savanna is known to be of anthropogenic origin. Evidence from the fossil pollen record suggests that it is highly unlikely that the remaining savanna—that lacking archaeological evidence of human disturbance—is naturally occurring. If all savanna vegetation is considered anthropogenic, then 26% of Palau's volcanic terrain is inferred to have undergone substantial habitat decline without recovery (Supplementary Data 6). When the decline in habitat includes areas known to have been re-forested after human disturbance, an additional 13% of Babeldaob's habitat has undergone a directly quantifiable historic fluctuation, making the overall total of inferred native habitat decline in Palau is 39%. This conservative inference (5b) is strongly supported since the total extent of proven habitat decline is 31% (5a).

The evidence presented here would qualify all endemic plants restricted to forest habitat on Palau's volcanic terrain for IUCN status of Vulnerable; a total of 31-39% in historic habitat decline or fluctuation meets the requirements of Criterion A. However, extending the time considered for these changes beyond three generations does not enable the assessment of these species with IUCN Criteria. Our proposed alternative methodology however, removes this time constraint enabling Palau's volcanic island restricted endemic plants to be listed as "At Risk (Priority Level 2)."

3.7 Globally recognizing threatened status of species

We suggest that the neglect of historical evidence beyond three generations is a fundamental weak point in the use of IUCN criteria for assessing plant species in many tropical regions, and concur with Regnier et al. (2009) that the IUCN Criteria are more suitable for vertebrates. Most vertebrate groups are more completely known than plants, benefiting from a larger ecological-based literature. The threatened status of both plant and invertebrate species relies primarily on the taxonomic literature, which is sparse in most tropical regions. In the case of Palau, there are known endemics with ranges substantially smaller then the total documented deforested land area (Costion et al. 2009). The 115.6 km² of area proven disturbed by Liston et al. (2011) could have maintained habitat for over half the population of some of these endemic species. Even though a small proportion of this area has subsequently re-forested, loss of habitat in the tropics or biodiversity “hot spots” is a more serious concern than in temperate areas or “cold spot” regions, which are known to be more resilient and able to re-forest with minimal or no species loss (Pimm et al. 1995). Palaeocores document unidentified fossil pollen types present before Palau was colonized and absent after the advent of humans (Athens and Ward 2002, 2005). Endemic plant species may have gone extinct and the extent of occurrence of others may have declined substantially in response to human activities. This could potentially explain some of the disjunct and scattered distributions of some of Palau’s endemic plants.

In the Pacific few quantitative studies have yet to be initiated for plants and conducting them comprehensively by 2020 is a far from realistic target. An approach, such as the one suggested in this paper, that considers evidence of population declines over much longer periods, is informative about the status of species under consideration and can be done utilizing existing data. This information can then be weighted against the likelihood of extinction from current threats. This method may prove to be useful on other islands in the Pacific and beyond where researchers and policy makers struggle with the same data limitations. Whilst the method developed here can be applied to a range of bioregions, it may require modification and adaption to specific biomes with differences in the availability of data. In many bioregions, however the data required for the application of this methodology already exists and will only require the necessary collaboration of qualified researchers from the respective disciplines.

Local governments can devise new criteria for assessing threatened status of their own species that are more flexible than the IUCN “one size fits all” model. The United

States Endangered Species Act of 1973 is an example of a dynamic system that allows for petitioning of species for consideration to the list using any available evidence that suggests the species of concern is threatened with extinction or is considered "at risk." Recently, 48 species of plants endemic to the Hawaiian island of Kaua'i were added to the US Endangered Species List (US Fish and Wildlife Service 2010). The assessment process for these species utilized a similar ecosystem level approach, as in the present study, where an entire ecosystem or vegetation type was quantified and classified as threatened. Such an approach is likely to prove to be more practical in areas where little quantitative data is available for populations of species that are clearly vulnerable to extinction and could easily be adapted to local legislations or tribal laws where appropriate.

4. CONCLUSIONS

Despite widespread acknowledgment of the need to accelerate threatened assessments of plant species, the process is largely impeded by both the IUCN assessment criteria's high standards and the paucity of high-resolution distribution data for plant species in tropical regions where the majority of plant diversity occurs. To achieve the GSPC 2020 targets it is essential that either revisions be made to the existing IUCN criteria that would facilitate a more rapid assessment of plants species in these regions or, that the adoption of alternative plant assessment methodologies are widely recognized. We present one possible solution for the latter option by enabling the use of historic and archaeological evidence of landscape change and disturbance. On Palau's volcanic islands, evidence of ancient and historic land use identifies human activity deforesting a bare minimum of 31% of Palau's volcanic terrain. Although the direct affects of this deforestation on the endemic plant species are unknown it is certain to have caused reductions in their original population sizes.

In this study we also addressed a long debated hypothesis on the anthropogenic origins of Palau's savanna vegetation using an interdisciplinary approach. While the palaeoenvironmental record lends robust support, both substantial quantifiable archaeological and cartographic data and the lack of taxonomic evidence for a clear endemic savanna component strongly substantiates the savanna vegetation as primarily anthropogenic. Open savanna type vegetation may have existed in the Northern Marianas, which have a recent volcanic history, prior to human settlement. However, the data indicates that before colonization, Palau was an essentially a forested landscape with probably very few pockets of open terrain. At present, there is little support from existing species level data for the climate driven savanna origin theory in Micronesia.

This study raises questions with major implications for not only the Pacific but the field of biodiversity conservation at large. Can the threatened status of extant populations of plant species be assessed accurately when only three generations of their evolutionary history are considered? What are the affects of ancient and historic forest clearance and subsequent re-vegetation to biodiversity on islands? Should re-vegetated ancient sites whose current habitat appears natural be given equal biodiversity value as potentially undisturbed habitats? Beyond traditional archaeological field survey, what practical methods are available to identify these anthropogenic habitats? And, perhaps most importantly, since palaeoenvironmental and archaeological investigations capture key information and lessons about past land-use practices and human adaptations to changing environmental conditions should environmentalists and ecologists not be utilizing data from these fields of research to inform current conservation policies and decisions?

ACKNOWLEDGEMENTS

We thank the Critical Ecosystem Partnership Fund (CEPF) for funding this project and all those who contributed ideas and comments to the development of the manuscript including James Miller, Mike Balick, Art Whistler, Stephen Athens, Yoji Kurata, Satoshi Osawa, Mikiko Ishikawa, Susan Laurance, and Kirk Costion.

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SUPPLEMENTARY DATA

1. Data sources for island diversity data

New Guinea: (Johns, 1995, pers. comm 2010)
Norfolk Island: (Green 1994; Lange et al. 2005)
Samoa: (Whistler 1992, 2011a)
Tonga: (Whistler 1992, 2011b)
Solomon Islands: (Pippard 2008)
Vanuatu: (United Nations Environment Programme 1998)
Micronesia: (Fosberg et al 1979, 1982, 1987; Costion & Lorence 2011)
Fiji: (Watling 2005)
New Caledonia: (Lowry 1998)

2. Methods – Additional Information

1) We chose to exclude all plants endemic to limestone substrates in the present study. There is inadequate data from both the palaeoenvironmental and archaeological records to assess patterns of historic landscape change on the limestone islands. Hence, those plants endemic to limestone substrates, and plants classified as generalists, occurring on both volcanic and limestone substrates, were excluded.

2) Large increases in quantities of savanna-associated pollen are interpreted as evidence for savanna expansion and a decline of forest habitat (Athens and Ward 2005). The time period of this trend was noted across numerous studies across the Pacific regardless of the author's interpretation of cause. Archaeological evidence of vegetation disturbance lies in the construction of expanses of ancient monumental earth architecture and early 20th century agricultural pursuits that would have stripped the forest bare. The literature on the origin of the savanna vegetation in Micronesia was then reviewed with consideration to the island's age.

3) See main text.

4(a) Previously undocumented earthwork sites were recognized when in savanna through light-and-shadow contrast in georectified 1947, 1971 and 1976 aerial photographs and when hidden beneath forest canopy through pedestrian survey (Liston 2011). As forested sections of many difficult to access areas in the island's interior have yet to undergo archaeological survey, a conservative estimate of the area of unrecorded earthwork sites was made. Identification of Japanese era (1914-1944) land clearance was derived from a 1921 Japanese Army Land Survey Office map that carefully plotted Babeldaob's land cover, a 1954 USGS topographic map constructed from 1947 aerial photographs, and georectified 1947 aerial photographs (Iida 2011). This site data supplied direct evidence for large-scale transitions in land cover resulting from ancient and historic development activities (Liston et al. 2011).

4(b) Taxonomic evidence was compiled by reviewing all known publications relevant to the candidate taxa. See references below for a complete list.

5(a) Earthworks and Japanese era plantations found in open savanna and closed canopy forest were differentiated and quantified to distinguish between re-covered and un-recovered forest habitats (Liston et al. 2011). This assessed the amount of directly verifiable ancient and historic habitat decline or fluctuation.

5(b) All recognized vegetation categories from Palau are qualified as disturbed or intact habitat and quantified (Supplementary Data 6). Archaeological and cartographic evidence of past landscape history calculated from Liston et al. (2011) is then incorporated into the total calculations to provide the total extent of inferred habitat decline.

6) See main text.

3. Review of archaeological and palaeoenvironmental literature

In Palau the lack, or minimal distribution, of grasses, ferns, and other savanna vegetation such as Poaceae, *Lycopodium*, and *Pandanus tectorius* in the fossil pollen/spore record strongly suggests the volcanic islands were almost entirely forested prior to about 4300 calBP (Athens and Ward 2002, 2005; Athens and Stevenson 2010). They posit that the spike in savanna indicators at this time, along with the dramatic increase in microscopic charcoal particles, demonstrates human expansion on Babeldaob, likely for slash-and-burn cultivation. Sediment cores collected on Guam and the Northern Marianas also exhibit a significant correlation between likely human colonization and expansion and a substantial rise in grassland taxa and charcoal particles (Athens and Ward 1998, 2004; Athens et al. 2004). Although there is no archaeological evidence of human presence on the islands until about 1000 years later, the palaeodata, sensitive to environmental changes, serves as proxy evidence for human impacts (Kirch and Ellison 1994; Athens and Ward 2004). Due to low populations, sea level changes, island subsidence and numerous other factors, archaeological identification of the earliest sites is notoriously elusive.

An increase in fire frequency, identified by a dramatic rise in microscopic charcoal particles, can only result from the onset of aridity or by large-scale human activities such as forest clearing. Athens and Ward (2004, 2005) demonstrate the lack of synchronicity in the timing of early savanna formation within Palau and between Micronesian islands which they suggest is best explained by differentially distributed settlements and activity areas (Table S1). If climate change were the cause of the expanding grasslands, the palaeo-disturbance indicators would be expected to temporally coincide. A temporal variation for the onset of savanna expansion is also found when comparing islands across the Pacific although in this case more localized climate change could play a part.

Table S1. Vegetation changes suggesting human activity on Oceanic islands (partial data from Athens and Ward 2005).

Island	**Timing of Vegetation Changes (BP)**	**References**
Palau	4500/4300	Athens and Ward 2002, 2005; Athens and Stevenson 2010
Guam	4300	Athens and Ward 2004
Yap	3300	Dodson and Intoh 1999
Kosrae	2000	Athens et al. 1996
Mangaia, Cook Islands	2500 or 1600	see Anderson 1994
Pohnpei	2500-2300	Ayres and Haun 1990
Atiu, Cook Islands	1310	Parkes 1997
Rapa Nui	1200	Flenley 1994
New Zealand	800 or 1000	McGlone 1989; Newnham et al. 1989; Striewski et al. 1994

Athens and Ward (2002, 2005) also note that several unknown pollen types recorded in Palau’s palaeocores from pre-human times rapidly decrease, some to disappear entirely, after colonization. Similar findings are identified on Kosrae where the entire lowland vegetation was replaced by agroforest within about 500 years of human settlement (Athens et al. 1996). On O’ahu, a similar scenario occurred although the loss of forest is due to a complex of variables probably related to the introduction of the Pacific rat (*Rattus exulans*) (Athens and Ward 1993; Athens 1997, 2009; Athens et al. 2002). The Pacific rat may have also played a key role in the demise of native vegetation on Micronesian islands.

Other authors, notably Hunter-Anderson (2009; Zan and Hunter-Anderson 1987), argue that Pacific island savannas developed by natural means during the drier climate of the Pleistocene and fluctuated in size throughout the Holocene due to climate changes, edaphic conditions and natural fires. In this geoclimatic model, Hunter-Anderson emphasizes the presence of charcoal in the fossil record long before possible human colonization, discrepancies between the palaeoenvironmental and archaeological record, and presents possibilities related to soil conditions and climate, particularly the El Niño/Southern Oscillation (ENSO) weather system, for the documented changes in sedimentation and vegetation. She argues that the “Pleistocene savanna corridor” which has been inferred for the Sunda Plate in Southeast Asia (Bird et al. 2005) would have undoubtedly also affected the Mariana Islands with a drier Holocene climate causing the expansion and contraction of forests and savannas at different intervals.

Hunter-Anderson's geoclimatic model provides no explanation for how fires would have naturally ignited without a human presence, but more importantly does not address the work of Athens and Ward (2005), which demonstrated that charcoal and lignite cannot be distinguished in palynological sequences. The natural occurrence of lignite, Athens and Ward (2002) argue, explains the very low concentration of "charcoal" in the pollen record until colonization. Their argument is well supported by the significant increases in both charcoal particles and particle size coinciding with increases in pollen from savanna plants. However, even if climate change did cause fires and pre-human savanna formation, the only evidence available from Micronesian palaeocores is from the start of the Holocene onwards, thus Hunter-Anderson's inference of a parallel trend between the SE Asia corridor and Micronesia is based entirely on speculation.

A crucial component of the geoclimatic model is the existence of plants that are allegedly endemic to the savanna vegetation. These species are considered proof for the natural origin of savannas despite the lack of evidence for exceptionally recent and rapid speciation events. A few endemic plant species do occur in Micronesian savannas, however no molecular studies have been conducted to elucidate their evolutionary histories. We address this argument by reviewing the existing knowledge of all plant species that are known to be potentially endemic to Micronesia's savanna vegetation.

4. Review of taxonomic data

Mueller-Dombois and Fosberg (1998) list seven species that are potentially restricted to Micronesian savannas: *Dimeria chloridiformis, Geniostoma micranthum, Hedyotis korrensis, Ischaemum longisetum, Myrtella beningseniana, Phyllanthus saffordii* and *Timonius nitidus*. Hunter-Anderson (2009) provides an additional three taxa potentially endemic to Marianas savannas: *Glochidion marinanum, Hedyotis fruticosa* and *Timonius albus*. Three of the seven taxa Mueller-Dombois and Fosberg (1998) list—*Dimeria cholridiformis, Timonius nitidus* and *Geniostoma micranthum*—are no longer considered Micronesian endemics (Costion and Lorence 2011). Of the potential endemics proposed by Hunter-Anderson (2009), only *Glochidion marinanum* is endemic to the Marianas as *Timonius albus* is actually endemic to Yap (Costion and Lorence 2011). *Hedyotis fruticosa* was likely confused with *Hedyotis fruticulosa* since the former, native to South Asia, does not occur in Micronesia. However, both Fosberg et al. (1993) and Stone (1970) doubted the presence of *H. fruticulosa* in the Marianas with the former determining that Marianas' collections of *H. fruticulosa* to actually be *H. laciniata*.

Table 2 (main text) shows that four of the remaining seven proposed savanna endemics are known to occur both in savanna and other native habitats. *Glochidion marinanum* and *Ischaemum longisetum* occur on limestone (Stone 1970); *Myrtella bennigseniana* is found in disturbed areas; and *Hedyotis korrensis*, the only proposed savanna endemic species restricted to Palau, occurs on exposed volcanic rock outcrops. The habitat of the Yap endemic, *Timonius albus*, is unknown. This leaves two candidate savanna endemics—*Phyllanthus saffordii*, *Hedyotis laciniata*—both of which lack evidence for a solid habitat restriction to the extant savanna vegetation. *H. laciniata* is restricted to volcanic areas of the Northern Marianas and *P. saffordii* is closely related to *P. palauensis* which commonly occurs on basalt rock outcrops.

To the list of seven remaining candidate endemic Micronesian savanna taxa, we assess nine additional Palau endemic species associated with savanna habitat (Table 3, main text). At least six of these species occur in native habitats other than savanna. *Phyllanthus palauensis* is also found on basalt rock outcrops while *Morinda pedunculata, Timonius subauritus,* and *Trichospermum ledermannii* are savanna shrubs or small trees that are also commonly located along forest-savanna borders and forested ridgelines unrelated to savanna (Costion and Kitalong 2006). Additionally, *Trichospermum ledermannii* frequently occurs in disturbed sites accompanying forest re-growth and is found on exposed rock outcrops. *Hedyotis korrorensis* and *Hedyotis tomentosa* are both characteristic of Palau's savanna vegetation and are well-supported endemics. *H. korrorensis* is recorded from both exposed rock outcrops and the forest-savanna edge ecotone (Costion and Kitalong 2006). *H. tomentosa* has been collected from deeply weathered volcanic areas and from the island of Oreor that does not contain savanna habitat (Fosberg et al. 1993).

The remaining four species listed in Table 3 lack sufficient evidence to prove that they are restricted to savannas and some may not even be distinct species. *Hedyotis aimiriikensis* is a doubtful species only known from the type collection, which has not been manually inspected since 1936 when Hatusima (1936) reduced it to a synonym of *H. korrorensis*. Fosberg et al. (1993) resurrected the name but provided no additional collections or support for doing so. *H. korrorensis* is very variable in morphology with four varieties recognized by Fosberg et al. (1993), none of which are currently accepted (World Checklist of Selected Plant Families 2011). *Hedyotis sachetiana* is also a doubtful species, known only from the type, which lacks flowers. It was distinguished from *H. tomentosa* (Fosberg et al. 1993) primarily by general vegetative differences, which, on the basis of only one collection, is not convincing. *Hedyotis suborthogona* is only known from the type and one additional collection and may be synonymous with *H. fruticulosa* from which it differs on the basis of minor morphological characters (Fosberg et al. 1993). Additional collections and work are needed to confirm its status as a savanna endemic. Virtually nothing is known of Palau’s alleged endemic grass, *Panicum palauense*. More collections and data on its ecology and habitat are required before the species can support any hypothesis.

Our review of the taxonomic and endemic status of plants allegedly endemic to savannas in Micronesia supports the idea posed by Fosberg (Mueller-Dombois and Fosberg 1998) and Manner et al. (1999) that savannas were previously restricted in extent possibly to volcanic slopes in the Northern Marianas. The known distribution of *Hedyotis lacinata*, only occurring in savanna on these volcanic slopes, possibly supports this notion. Volcanic slopes contain rock outcrops and are periodically exposed to natural fires and landslides. These recurring disturbances maintained niches for plants that are currently primarily found in savanna habitats. In other regions of the globe, aridification of wet forest caused by climate change led to large-scale speciation events. Australia is a classic example; massive species radiation in the dry sclerophyll flora began in the

Miocene and developed over millions of years as rainforest contracted across the continent (Crisp et al. 2004). The lack of diversity in Micronesia's endemic savanna species supports a recent origin or expansion of the vegetation type from a restricted extent.

5. Review of support for natural regeneration of Palau's forests

Forest regeneration studies document that Palau's volcanic island forests recover from human disturbance. For the Ngeremeduu Bay area on Babeldaob's west coast, Endress and Chinea (2001) showed a 10.9% increase of forest cover at a rate of 0.22% per year and a 11.2% decrease of savannas over a 45 year period (1947-1992). The documented areas of forest expansion were located primarily in abandoned Japanese agricultural sites adjacent to intact forest. In southeast Babeldaob, Kitalong (2008) reported an increase in forest size of 0.5% at a rate of 0.04 per year over a 13 year period.

Recent archaeological and palaeoenvironmental investigations in Palau also provide ample evidence for ancient forest loss and re-growth (see Liston et al. 2011). Pollen diagrams from palaeocores suggest an oscillating pattern of savanna formation and forest regeneration with intervals of forest re-growth at c. 2500 BP and again at c. 600 BP (Athens and Ward 2005). The latter period of forest regeneration roughly coincides with the shift in settlement pattern out of the interior to the coastal margins.

6. Total inferred habitat decline

Intact and disturbed habitats on Palau's volcanic islands, derived from the Cole et al. (1987) vegetation survey, are quantified in Table S2. Vegetation categories are presented for Babeldaob and the other high volcanic islands (Malakal, Oreor and Ngerekebesang). Intact and disturbed habitats are calculated separately. The grassland category is equivalent to savanna and, following the premise presented here, is grouped with disturbed habitats. Archaeological data strongly suggests that the majority of Babeldaob's marsh lands are a disturbed habitat associated with earthwork construction and use (Liston 2011). The near complete absence of endemic species occurring in this vegetation type supports this inference. Total hectares and percentages are given following Cole et al. (1987) and then modified by incorporating the archaeological and cartographic evidence of past landscape history calculated in Liston et al. (2011). The 49 km^2 listed for re-forested earthworks include both the documented and the estimated minimum area of undocumented earthworks.

Table S2. Intact and disturbed habitats on Palau's volcanic islands, in hectares (after Cole et al. 1987).

Intact Habitats	**Babeldaob**	**Other volcanic high islands**	**Disturbed Habitats**	**Babeldaob**	**Other volcanic high islands**
Upland forest	21 690	201	Plantation Forest	24	2
Swamp forest	1,617	15	Agroforest	924	6
Mangrove forest	4,025	205	Secondary Vegetation	515	79
Fresh water	15	9	Marsh (fresh water)	448	>1
Palm forest		>1	Marsh (cultivated)	107	2
Subtotals	27 347	430	Grassland	6,728	53
			Croplands	140	87
			Urban lands	247	295
			Barren	149	5
			Subtotals	9,282	530
Subtotal	**27 777 = 74%**		**Subtotal**	**9,812 = 26%**	
Re-forested earthworks	*- 4,900*		*Re-forested earthworks*	*+4,900*	
Total	**22 877 = 61%**		**Total**	**14 712 = 39%**	

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CHAPTER 3

The Endemic Plants of Micronesia: A Geographical Checklist and Commentary

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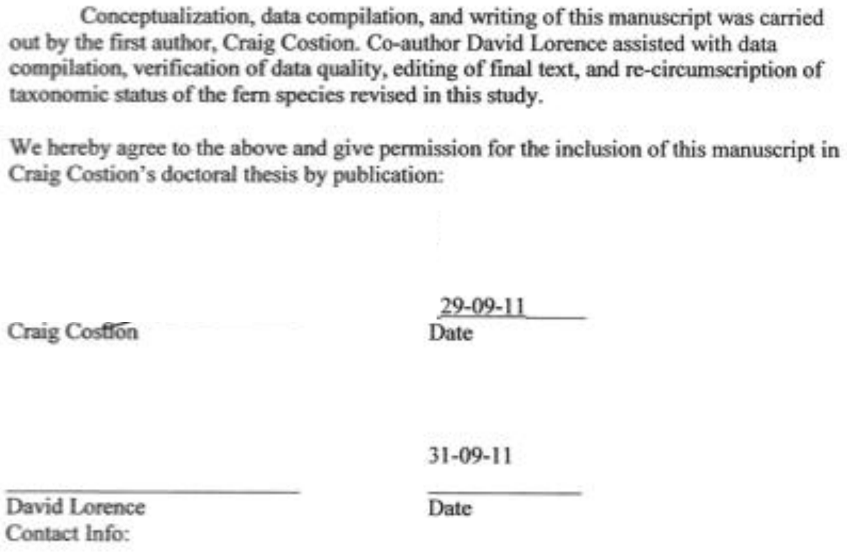
Micronesica 42(1): 51-100, 2012

Declaration of authorship



Conceptualization, data compilation, and writing of this manuscript was carried out by the first author, Craig Costion. Co-author David Lorence assisted with data compilation, verification of data quality, editing of final text, and re-circumscription of taxonomic status of the fern species revised in this study.

We hereby agree to the above and give permission for the inclusion of this manuscript in Craig Costion's doctoral thesis by publication:

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ABSTRACT

The Micronesia-Polynesia bioregion is recognized as a global biodiversity hotspot. However, until now estimates regarding the number of endemic plant species for the region were not supported by any comprehensive published work for the region. The results of this study indicate that Micronesia has the world's highest percentage of plant endemism per square kilometer out of all globally recognized insular biodiversity hotspots. A checklist of all endemic plant species for Micronesia is presented here with their corresponding geographical limits within the region. A summary of previous work and estimates is also provided noting the degree of taxonomic progress in the past several decades. A total of 364 vascular plant species are considered endemic to Micronesia, most of them being restricted to the Caroline Islands with a large percentage restricted to Palau. The checklist includes seven new combinations, one new name, and two unverified names that require additional study to verify endemic status. Overviews of each respective botanical family represented in the list are given including additional information on the Micronesian taxa. Recommendations for future work and potential projects are alluded to throughout the text highlighting major data gaps and very poorly known taxa. The following new combinations and names are made: *Cyclosorus carolinensis* (Hosokawa) Lorence, **comb. nov.** , *Cyclosorus gretheri* (W. H. Wagner) Lorence, **comb. nov**., *Cyclosorus guamensis* (Holttum) Lorence, **comb. nov**., *Cyclosorus palauensis* (Hosokawa) Lorence, **comb. nov.** , *Cyclosorus rupiinsularis* (Fosberg) Lorence, **comb. nov**., *Dalbergia hosokawae* (Hosokawa) Costion **nom. nov.,** *Syzygium trukensis* (Hosokawa) Costion & E. Lucas **comb. nov.**.

INTRODUCTION

The word Micronesia, derived from Greek for “small islands,” is geographically apt. This bioregion spans a region of the Pacific Ocean comparable in size to the continental United States, or Australia, but the total land area of all the islands within this area sums to roughly 2,628 km². If all the islands of Micronesia were compressed into one land mass it would comfortably fit within the US state of Rhode Island. The sizes of the islands however, do not come even remotely close to reflecting the wealth of biodiversity they contain. The results of the present study indicate that Micronesia contains a higher percentage of endemic plant species per square kilometer land area than the Hawaiian archipelago by ten orders of magnitude. Despite this distinction, their remoteness has rendered them under-studied and for the most part un-noticed. The paucity of studies in the region is compounded by its complex geology, having six distinct geological subregions of ages varying from up to 97 million years old in the Marshall Islands, the oldest coral islands and atolls on earth (Coppers 2009), to more recent volcanic events of < 1 million years old in the Northern Marianas (Trusdell 2009). The combination of old age and close proximity to continental land masses of some of the Micronesian islands has enabled them to accumulate a very high richness of distinct plant lineages compared to more remote archipelagos such as Hawaii. The available terrestrial habitat in Micronesia is literally packed with biodiversity, much of which is only known from a few collections.

Micronesia, defined here as the Caroline, Mariana, Gilbert and Marshall Islands, (Figure 1) is part of the Polynesia-Micronesia global biodiversity hot-spot (Conservation International 2007). These global biodiversity hotspots were determined primarily on the basis of the number of endemic plants contained within them and their degree of threat. Despite Micronesia’s noteworthy biodiversity and its long recognized importance for conservation, a complete checklist of endemic plants for the bioregion has been lacking until now. The present study aims to fill this gap by synthesizing all existing taxonomic literature to date for the region. All previous studies have relied entirely on estimates of the number of endemic plants for Micronesia. Estimates on quantity of endemic species may help address global priorities but the lack of a checklist of endemic plant species has prevented an assessment of species that are threatened and in need of priority for local conservation measures. Studies have shown that the Polynesia-Micronesia biodiversity hotspot is the most vulnerable of all the world's biodiversity hotspots to extinctions due to its insular nature (Baillie et al. 2004), and thus such a list is far over-due.

The present study draws primarily upon the extensive work of the eminent Pacific botanist Francis Raymond Fosberg (1908-1993) his collaborator Benjamin Stone (1933-1994), and the work of recent Pacific botanists. Fosberg provided a number of the endemic plants that occur in Micronesia in the abstracts of his geographical checklists (Fosberg et al 1979, 1981, 1987) but did not clearly indicate which taxa he considered endemic. All species listed in the checklists included their known distributions within Micronesia, yet confusion over whether these distributions were considered global or only the distributions of listed taxa within the Micronesia bioregion has abounded ever since. Fosberg's estimates have been routinely utilized subsequently without further taxon specific and wider geographic verification. We can only speculate why Fosberg indicated that he knew how many endemics that occur in Micronesia but did not differentiate between true insular endemic taxa and species restricted to one archipelago in Micronesia but with wider representation elsewhere. This was done for the families covered in the Flora of Micronesia (Fosberg & Sachet 1975a, 1975b, 1977, 1980a) so it is likely that this task was saved for treatment in in the flora family by family where species concepts could be covered in greater depth. It is also possible that he hoped to inspire someone else to take on this substantial task. Whether or not the latter reason is true we cannot say, but we can say that this was the effect it had. The present study is the final product of an effort extending over seven years that began with the realization of this problem and fundamental gap in knowledge for Pacific botany.

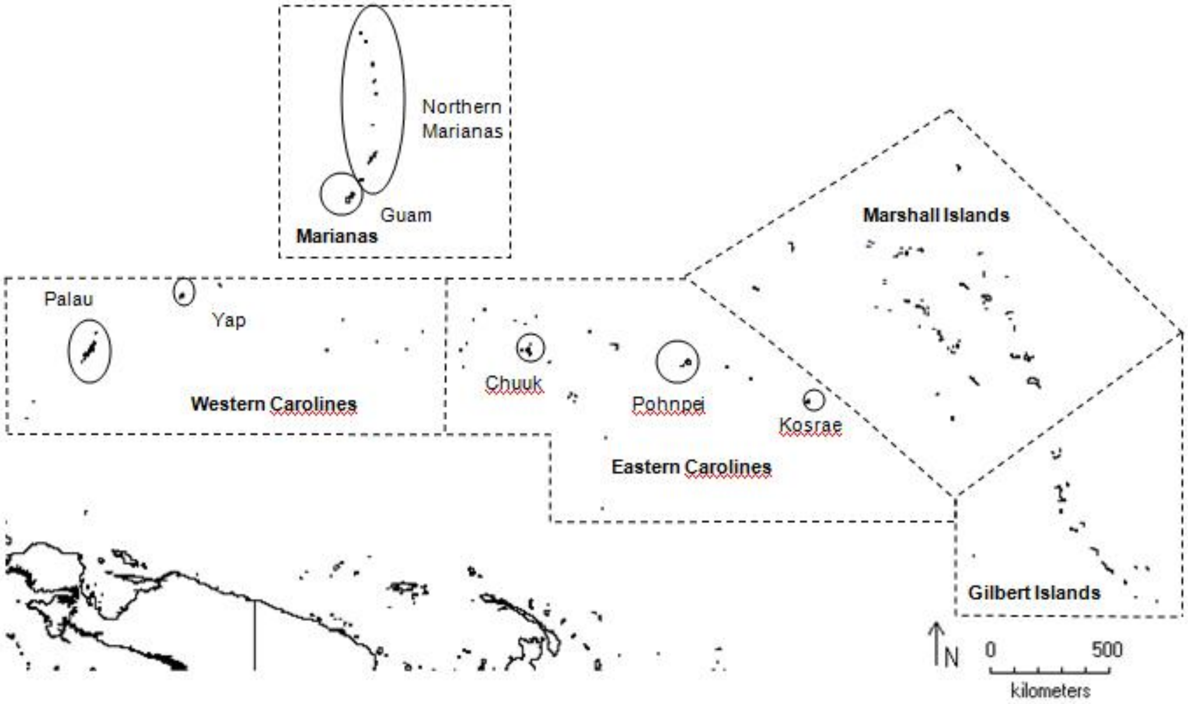
This "problem" however is old news for the Pacific. No less than 30 years ago, Benjamin Stone (1970) lamented in the introduction to his Flora of Guam that the production of a large volume such as a flora or checklist for a bioregion, often only the first stage of coming to grips with a flora and the biota it sustains, usually leads to the end of floristic research for that region. Though it can certainly be said that Fosberg and his colleagues proved him wrong in this regard, there was perhaps a grain of truth in Stone's statement. Aside from the baseline work of Fosberg and his collaborators much of the Micronesian flora remains very poorly studied and understood taxonomically. Many of the species Fosberg described have since become synonymized; others have yet to be verified, being known only from the type collection. Some of these have not even been collected since before WWII.

Stone (1970) commented on this very slow process of taxonomic revision that over the course of decades, leads to new species concepts. This of course directly affects our understanding of what is and what isn't endemic to a region. As Stone correctly predicted, several of Guam's vascular plant species that he treated as endemic, 22% of the total, are no longer considered to be so. Our reassessment concludes that there are about 11 vascular plants endemic to Guam, including two pteridophytes and nine angiosperms. They are as follows: *Ceratopteris gaudichaudii* Brongniart, *Cyclosorus guamensis* (Holttum) Lorence, *Dianella saffordiana* Fosberg & Sachet, *Bulbophyllum guamense* Ames, *Potamogeton marianensis* Cham. & Schltdl., *Eugenia bryan*i Kaneh., *Phyllanthus mariannensis* W.L. Wagner & Lorence, *Hedyotis megalantha* Merr., *Psychotria andersonii* Fosberg, *Psychotria malaspinae* Merr., and *Elatostema stenophyllum* Merr.. Thus the long delay for the checklist presented here may have actually been fortuitous. Though we do expect this slow process to continue, requiring eventual revision of our list, we do feel that sufficient taxonomic progress has been made in the last two decades to warrant an authorative list. More importantly, we feel that from a conservation perspective this information is absolutely crucial for guiding policy and helping establish priorities for small island nations with limited resources and funding and that further delay could lead to more unnecessary extinctions in the already compromised Pacific biota.

Although our checklist substantially reduces the number of endemic species that were estimated for Micronesia previously it in no way downlists Mirconesia as a globally important biodiversity hotspot. If anything, now residents in their respective islands will be better informed to prioritize local efforts and actions. Flagging such a huge bioregion as globally important can help raise international attention and funds, but applied conservation can only take place locally. This is especially true in Micronesia which spans millions of square miles of ocean and is divided into six nations or territories further split into at least ten major island state governments each with numerous regional tribal governments. We hope this checklist will serve to help do just that. To better enable this we have organized the checklist with the users in mind, avoiding jargon and technical terms wherever possible and providing a document that is well balanced between providing as much technical data as possible without losing the captive interest of readers by also including some more general facts and notes about plant identification, uses, and biogeography of the region.

All species listed here are considered endemic to Micronesia or otherwise to island groups or single islands within Micronesia (Figure 1). We define endemic as a species that has a geographical range restricted to the region specified here. We classify species as endemic to Micronesia (occurs in the Carolines and Marianas), the Carolines (occurs on at least one island in both the Eastern and Western Carolines), the Marianas (occurs on the Southern and Northern Marianas), the Gilberts (excluding the other islands of the Republic of Kiribati), the Marshalls (endemic to the Republic of the Marshall Islands), the Southern Marianas (Guam, Rota, Tinian, and Saipan), the Northern Marianas (all islands north of Saipan in the Commonwealth of the Northern Mariana Islands), the Western Carolines (occurs on the Palau and Yap archipelagos), the Eastern Carolines (occurs in more than one of the following island states: Chuuk, Pohnpei, and Kosrae), and finally species endemic to the island nations or states of Guam, Palau, Yap, Chuuk, Pohnpei, and Kosrae. In addition, when known, we have classified species that are restricted to specific soils within these categories. Species are either restricted to volcanic soils (V), limestone soils (L), have a generalist habit occurring on both (G), or are aquatic (A).

Figure 1: Geographical boundaries of major island groups in the Micronesia region



We also list the growth forms of species to the best of our knowledge. Species are categorized as either one or two of the following growth forms: herb (H), epiphyte (E), herbaceous vine (HV), woody liana (WL), shrub (S), tree (T), canopy tree (T(c)), and understory tree (T(u)).

A relative rarity index is provided based on a combined assessment of our knowledge of the flora and review of the literature. We provide these data well aware that our knowledge of rarity is far from complete, and hope that the blanks in this or any of the other columns will inspire others to fill them in. In any case, for the species that we do know sufficiently, the relative rarity index can help identify immediate conservation priorities. We classify species as either one or a combination the following qualitative categories:

Dominant (D) = Forms a dominant layer of at least one plant community in Micronesia
Common (C) = Occurs frequently and throughout its known range

Uncommon (U) = Occurs throughout its known range but not in abundance
Rare (R) = Is very uncommon or has been rarely encountered, its range is not well known
Range Restricted (RR) = Its distribution is known to be restricted to a very small area

The example below indicates that the species is a common liana or woody vine, is endemic to Yap, and is restricted to limestone soils. A complete key to the coding scheme is provided in Table 1.

Taxon Name	**Endemic to**	**Soils**	**Form**	**Rarity**
Genus species Author	Yap	L	WL	C

Table 1: Soil type, growth form, and relative rarity index coding key

Code Definition	Soils	Form	Rarity
Volcanic	V	--	--
Limestone	L	--	--
Generalist	G	--	--
Aquatic	--	A	--
Herb	--	H	--
Epiphyte	--	E	--
Herbaceous Vine	--	HV	--
Woody Liana	--	WL	--
Shrub	--	S	--
Tree	--	T	--
Canopy Tree	--	T(c)	--
Understory Tree	--	T(u)	--
Dominant	--	--	D
Common	--	--	C
Uncommon	--	--	U
Rare	--	--	R
Range Restricted	--	--	RR

The checklist is organized taxonomically following the most recent Angiosperm Phylogeny Group (APG) classification, subdivided into Gymnosperms, Pteridophytes, Basal Angiosperms, Monocots, and Eudicots. Families are then arranged in alphabetical order, followed by genera and species in alphabetical order. Below each family name we have listed in the following order the number of native *genera/species(endemics)* known from that family for Micronesia. A description is included for each family to briefly introduce the family and provide any other useful and or interesting information for specific taxa where deemed appropriate. Information on the number of species per family and genus was obtained from the Angiosperm Phylogeny Website (Stevens 2001) unless otherwise noted. We follow the classification of Smith et al. (2006) for the family concepts and species numbers of the Pteridophytes (ferns and lycophytes).

Summary of Taxonomic Revision of Micronesia's Endemic Flora

A summary of revised percentages of Micronesia's endemic flora is provided in the following table (Table 2). Changes of endemic status can be grouped into two categories; changes made due to revised species concepts and changes made due to herbarium records found outside Micronesia for particular taxa. To confirm endemic status we reviewed the literature for Micronesia. Primary resources included the checklists of Fosberg et al. (1979, 1981, 1987) and all of his subsequent publications, the Flora of Guam (Stone 1970), Flora Malesiana, the Kew's World Checklist of Selected Plant Families (2010) online resource, and GrassBase (Clayton et al. 2002). Recent checklists have been published for Pohnpei (Lorence & Flynn 2009; Herrera et al. 2010). Another modern checklist exists for Palau (Hillman-Kitalong et al. 2008). We also scanned the the literature for family and generic level taxonomic revisions that applied to the Micronesian flora. Distribution records were scanned using additional online resources including the Global Biodiversity Information Facility (GBIF), herbarium records made available by request to the authors, or other reports and publications that cited distribution data. A complete list of species that were formerly considered endemic, such as in the Flora of Guam, with the accompanying citations or reasons for delisting is not provided here but is available upon request from the authors. If a species was listed in any of Fosberg's publications or the Flora of Guam, we checked its endemic status, though we do apologize if anything has escaped our attention and welcome corrections, new records, and updated species concepts from other researchers. Endemic subspecies and varieties are not included in this list. We also excluded phrase names or species only identified to genus level such as *Oberonia* sp. aff. *podostachys* Schltr. (Fosberg et al. 1987) to avoid falsely applying names of poorly understood or misidentified collections. Although we do expect new records and a few new species to be found in Micronesia, more cases of taxonomic revision over time are expected. This will lead to the incorporation of some currently recognized endemic species into broader species concepts and the opposite process of splitting widespread taxa into endemics with smaller distributions for others. This will require updating of our checklist periodically

Table 2: Summary of revised endemic species concepts for Micronesia

No. of Endemics in Former Treatment	**No. of Endemics in Current Treatment**	**Percent of Change**
Fosberg et al. (1979-1987)	Endemic to Micronesia	
Dicots (369)	Dicots (212)	Dicots: 43%
Monocots (166)	Monocots (121)	Monocots: 27%
Pteridophytes (31)	Pteridophytes (30)	Pteridophytes: 3%
Gymnosperms (0)	Gymnosperms (1)	
Total (566)	**Total (364)**	**Total: 36%**
Guam (Stone 1970)	Endemic to Marianas	
Total (69)	**Total (54)**	**Total: 22%**
Palau (unpublished estimates)	Endemic to Palau	
Total (200-260)	**Total (135)**	**Total: 32-48%**

RESULTS

Checklist of Endemic Species

Taxon Name	Endemic to	Soils	Form	Rarity

LYCOPHYTA
(6)

SELLAGINELLACEAE
1/7(6)

Sellaginellaceae can be overlooked being small, uncommon herbs, often occurring along rocky stream banks or moist rocky outcroppings. They are related to the Lycopodiaceae and together form a distinct lineage that branched off before the radiation of ferns. One species occurs along edges of savannas in Palau. *Selaginella kanehirae* is known from Pohnpei and Kosrae, and *S. volkensii* is known from Yap and Chuuk. The rest are endemic to specific island states with the exception of *S. ciliaris*, which is widespread in northern Australia and Southeast Asia. Currently, the relationships and species delimitations between the following taxa and the robustness of the species concepts are poorly understood and require further study.

Selaginella dorsicola Hosok.	Palau	V	H	--
Selaginella kanehirae Alst.	E. Carolines	V	H	--
Selaginella kusaiensis Hosok.	Kosrae	V	H	--
Selaginella palauensis Hosok.	Palau	V	H	--
Selaginella pseudo-volkensii Hosok.	Palau	V	H	--
Selaginella volkensii Hieron.	Carolines	--	H	--

PTERIDOPHYTA
(24)

CYATHEACEAE
1/3(2)

There are three native tree fern species in Micronesia, formerly placed in *Cyathea*. Two of them are considered endemic. They are both locally abundant but *Sphaeropteris aramaganensis* is only known from three small islands in the N. Marianas on high volcanic slopes. *S. nigricans* occurs commonly in open savannas and in the forest understory of the Caroline Islands. *S. lunulata* is less common, but also occurs in Southeast Asia.

Sphaeropteris aramaganensis (Kaneh) R. M. Tryon	N. Marianas	V	T	R
Sphaeropteris nigricans (Mett.) R. M. Tryon	Carolines	V	T	C

DRYOPTERIDACEAE
7/12(2)

Dryopterdidaceae is a diverse family with over 1,700 species worldwide. Although they are cosmopolitan they are most abundant in temperate regions and the higher elevation mountain floras in the tropics. *Elaphoglossum*, Greek for serpent tongue, is mostly a tropical group with over 600 species. It was formerly placed in Lomariopsidaceae. Only two endemic species are known from Micronesia. One of these, *E. kusaiense* is possibly a synonym of *E. carolinense*.

Elaphoglossum carolinense Hosok.	E. Carolines	V	H	--
Elaphoglossum kusaiense H. Ito	Kosrae	V	H	--

GLEICHENIACEAE
1/2(1)

The *Dicranopteris* ferns of Micronesia are associated with open savannas, roadside banks, and other clearings. They form very dense thickets, which are routinely burned by people to clear the way. This in turn prevents forest regeneration but also increases plant diversity in the savannas, as it is hard for other plants to compete with *Dicranopteris*. Fosberg's *D. weatherbyi* is distinguished from the common *D. linearis* by its much larger overall size of all parts. It is known only from Pohnpei and Kosrae, and was listed as vulnerable on the 1997 IUCN Red List of Threatened Species.

Dicranopteris weatherbyi (Fosberg) Glassman	Carolines	V	H	R

LINDSAEACEAE
3/12(1)

Lindsaeaceae is a small mostly tropical family with approximately 200 species. Its genera were formerly placed in Dennstaedtiaceae. Molecular data supports it as a monophyletic family and the most basal lineage in the Polypodiales. *Tapeinidium* is comprised of approximately 19 species, one of which, *T. carolinense*, is endemic to the Caroline Islands.

Tapeinidium carolinense Kramer	Carolines	V	H	C

LOMARIOPSIDACEAE
3/9(1)

Lomariopsidaceae is almost entirely restricted to the tropics, with about 70 species. They are characterized by having dimorphic leaves where the fertile parts are on one leaf, the other sterile. *Cyclopeltis* is a small genus with only about seven described species. *C. kingii* is a very poorly known species restricted to the limestone forests of Palau.

Cyclopeltis kingii (Hance) Hosok.	Palau	L	H-E	--

PTERIDACEAE

12/20(3)

Pteridaceae, or the brake fern family, is a large fern family that has gone through much revision, which is ongoing today. The family includes a number of genera that have been traditionally grouped into separate families. Relationships between genera remain unclear within the family which itself, as currently recognized, may not even be monophyletic. *Adiantum*, the maiden-hair ferns, a genus of about 200 species, are distinctive in appearance and favored in horticulture. They are commonly associated with stream banks and rock faces adjacent to waterfalls. *Ceratopteris* was traditionally placed in the monotypic Parkeriaceae comprised of only four to six aquatic species. They are widespread in the tropics and comprise the only genus of homosporous ferns that is entirely aquatic. The status of *C. gaudichaudii* as an endemic variety or species is currently under investigation (Masuyama & Adjie 2008). The genus *Pteris* has approximately 280 species worldwide with one Micronesian endemic represented by only a few collections. The name *Pteris* is derived from the Greek word for fern.

Adiantum palaoense C. Chr.	Palau	V	H	--
Ceratopteris gaudichaudii Brongniart	Guam	A	H	--
Pteris tapeinidiifolia H. Itô	Palau	L	H-E	--

POLYPODIACEAE

14/20(5)

Polypodiaceae has over 1,500 species, mostly tropical and epiphytic. Several traditional families have been incorporated into this larger circumscription of Polypodiaceae. About 20 species have been recorded from the Micronesian region. All four genera listed below were formerly placed in Grammitidaceae. *Calymmodon* is mostly an Indomalaysian genus of 25-30 species. *Grammitis* formerly contained about 200 species. Most of these have been transferred to other genera including *Ctenopterella*, *Oreogrammitis*, and *Prosaptia*, leaving *Grammitis* with about 25 species. *Grammitis ponapensis* will very likely be separated into a new genus that has yet to be described. *Prosaptia* contains approximately 50 species with Indomalaysian-Pacific distribution. Its name in Greek refers to its distinctive sori, “immersed or inserted” in the lamina.

Calymmodon ponapensis Copel.	Pohnpei	V	E	--
Oreogrammitis palauensis (Hosok.) Parris	Palau	V	E	--
Grammitis ponapensis Copel.	Pohnpei	V	E	--
Oreogrammitis scleroglossoides (Copel.) Parris	Pohnpei	V	E	--
Prosaptia palauensis Hosok.	Palau	V	H	--

THELYPTERIDACEAE

3/19(8)

Thelypteridaceae is a large, mostly tropical family with approximately 950 species. Most are terrestrial; a few are lithophytic or semi-aquatic. The taxonomy of this family has been problematic with no consensus on the correct circumscription of genera. Traditionally Micronesia's species have either been treated all under *Thelypteris* (Fosberg et al. 1982) or split into several separate genera (Holttum 1977). We follow the circumscription of Thelypteridaceae genera presented by Smith et al. (2006), and treat all of the Micronesian endemics under *Cyclosorus.*

Cyclosorus carolinensis (Hosokawa) Lorence	Palau	L	H	--
Cyclosorus perglanduliferus (Alderw.) Ching	Palau	V	H	--
Cyclosorus gretheri (W. H. Wagner) Lorence	S. Marianas	L	H	C
Cyclosorus guamensis (Holttum) Lorence	Guam	--	H	--
Cyclosorus maemonensis Wagner & Grether	Micronesia	--	H	U
Cyclosorus palauensis (Hosokawa) Lorence	W. Carolines	V	H	--
Cyclosorus ponapeanus (Hosokawa) Lorence	Pohnpei	V	H	--
Cyclosorus rupicola (Hosokawa) Lorence	Palau	L	H	--

WOODSIACEAE
1/6(1)

Woodsiaceae contains approximately 700 species circumscribed into 15 genera. Most species are placed within two genera including *Diplazium*. *Diplazium* contains approximately 400 species, though is likely a paraphyletic genus (Smith 2006). Its name is derived from the Greek diplazios, meaning double, referring to the indusia that lie on both sides of the lamina veins. *Diplazium ponapense* (Copel.) Hosok. may be synonymous with the older name *D. melanocaulon* Brack.

Diplazium ponapense (Copel.) Hosok.	E. Carolines	V	H	--

GYMNOSPERMAE
(1)

CYCADACEAE
1/2(1)

There are two native cycad species in Micronesia. One is considered endemic (Hill 1994; 2004), the other also occurs in Southeast Asia (DeLaubenfels 2007). These two species were formerly treated as one widespread species, *Cycas circinalis*, which is now regarded as endemic to the Western Ghats of India (Hill 2004). A more complete discussion on the history of this taxonomic problem was covered by Costion (2009). The local distribution of the two separate species that occur in Palau is not well known as they were formerly treated as one species. They can occur on all soil types but are more commonly found on sandy beach forest and on limestone islands. In the Marianas and to a lesser extent in the Rock Islands of Palau, *C. micronesica* can be abundant enough to form dense understory stands. Flour made from the seeds was often eaten by the indigenous Chamoro of Guam until it was suspected to be linked with the degenerative neurological disease known as

Guam dementia. Henceforth, consuming the seeds has been discouraged. However, the exact causes of the disease are to date, unresolved.

Cycas micronesica K.D. Hill	Micronesia	G	T-S	C-R

BASAL ANGIOSPERMS
(15)

ANNONACEAE
3/3(3)

Guamia was previously considered the only angiosperm genus endemic to Micronesia. Schatz (1987) revised this by describing a new species of *Guamia*, *G. mexicana*, from Mexico. The Guam species, however, is retained as an endemic species. It occurs abundantly on limestone soils in the Marianas, and occasionally on mixed soils. Both Annonaceae species from Palau are very poorly known and likely quite rare. *Polyalthia merrillii* may be only known from the type. *Goniothalamus carolinensis* is only known from the island of Babeldoab from a few collections. Notes from herbarium collections indicate that even the early Japanese collectors regarded it as a rare and uncommon tree.

Goniothalamus carolinensis Kaneh.	Palau	V	T	R
Guamia mariannae (Safford) Merrill	Marianas	G	T	A
Polyalthia merrillii Kaneh.	Palau	L	T	--

LAURACEAE
2/4(2)

Cinnamomum is a pantropical genus with approximately 250 species distributed throughout the Neotropics, Pacific, and Australasia. *Cinnamomum* and other members of this family are regarded as characteristic components of neotropical montane cloud forest canopy. Micronesia is notably home to the lowest elevation cloud forests in the world, occurring on the islands of Pohnpei and Kosrae. Both Micronesian species of *Cinnamomum* occur on Pohnpei. *Cinnamomum carolinense* is also known from Kosrae and Palau, but in Palau it is rare. On the island of Pohnpei, the leaves of native *Cinnamomum* species are boiled to make a delicious tea that has reported medicinal qualities. The only other native Lauraceae in the region belongs to *Cassytha*, a parasitic group of plants mostly of Australian distribution. *Cassytha filiformis* is a cosmopolitan species, which commonly occurs in the savannas and coastal areas of Micronesia.

Cinnamomum sessilifolium Kaneh.	Pohnpei	V	T	--
Cinnamomum carolinense Koidz.	Carolines	V	T	--

MYRISTICACEAE
2/3(1)

Myristicaceae is a pantropical family, though only a few species occur in Australia and the Pacific. *Horsfieldia* is represented by approximately 100 species, mostly in SE Asia with one species in Australia and a few species extending east to Micronesia and the Solomon Islands. *H. palauensis* is a common and characteristic component of Palau's volcanic upland and limestone forests. The widespread *H. irya* reaches its northeastern limit of distribution in Palau and Kosrae where it was formerly treated as the endemics *H. amklaal* and *H. nunu*. It is associated with fresh water and in Palau forms impressive stands of swamp forest in association with two *Calophyllum* species. *Horsfieldia tuberculata* was recorded for Palau under the previous name *H. novo-guineensis*; however it is very poorly known and rarely collected there. Local residents cannot distinguish it from the other two and some doubt it as a valid record. *Myristica insularis* was formerly regarded as endemic to the Carolines but was revised to be a variety *M. hypargraea,* a species also known from Samoa and Tonga, by de Wilde (1994). The author admittedly reported that limited material was studied ex situ and acknowledged morphological differences in the fruit and leaves but that the two were close enough to merit merging the taxa. Molecular studies may indicate otherwise and revive the endemic name.

Horsfieldia palauensis Kaneh.	Palau	G	T	C

PIPERACEAE
2/15(9)

Piperaceae are well represented and rich in endemics in Micronesia. Some species are well known while others are not and require further study (Fosberg & Sachet 1975). Both *Peperomia* and *Piper* are pantropical in distribution. *Peperomia* usually occurs as a terrestrial, epiphytic or lithophytic herb, while *Piper* often occurs as a shrub or hemiepiphytic vine. In *Peperomia*, *P. breviramula* occurs in the montane forest of Pohnpei and is known only from the type and one other collection. It is potentially the same species as *P. glassmanii,* which is also endemic to the Pohnpei mountain flora. *Peperomia kusaiensis* is epiphytic in the cloud forests of Kosrae, and *P. ponapensis* is lithophytic on limestone and basalt at low elevations in the Eastern Carolines from Chuk to the Marshall Islands. *Piper* is an important native plant genus for the people of Micronesia. *Piper betle* and *P. methysticum* are both used in the preparation of local intoxicants. Though the latter is only exploited in Pohnpei, the former is inseparable from daily life throughout Micronesia. *Piper nigrum*, black pepper, though introduced, has historical significance in the region where it was at one time a valuable commercial crop. Two species of *Piper* are endemic to Micronesia.

Peperomia breviramula C.DC.	Pohnpei	V	E	R
Peperomia glassmanii Yunck.	Pohnpei	V	E	--
Peperomia kraemeri C.DC.	Palau	G	H	--
Peperomia kusaiensis Hosok.	Kosrae	V	E	--
Peperomia mariannensis C.DC.	Marianas	L	H	--
Peperomia palauensis C.DC.	Palau	G	H	C
Peperomia ponapensis C.DC.	Micronesia	G	H	--
Piper guahamense C.DC	Marianas	L	S	C

Piper hosokawae Fosberg	Palau	G	WL	C

MONOCOTS
(121)

ARACEAE
6/9(2)

The arum or aroid family is mostly tropical and known for the calcium oxalate crystals or raphides present in most species. This explains the necessary preparations required for eating the main staple of most of Micronesia and Polynesia. Taro, a member of this family cultivated for its carbohydrate and nutrient-rich corms, has numerous varieties spanning four genera and several species. Many of these were introduced into the Pacific from Southeast Asia. Micronesia has two endemic aroids that occur as climbing vines.

Epipremnum carolinense Volkens	W. Carolines	V	H-E	C
Scindapsus carolinensis Hosok.	Chuuk	--	H-E	--

ARECACEAE
8/11(7)

Micronesia is home to eleven native palm species, seven of them endemic. Several of these palms have undergone recent name changes. *Ponapea* is a genus of only three known species, all endemic to Micronesia. It was formerly partially included under *Ptychosperma*. All three species of *Ponapea* are rare with the exception of *P. ledermanniana*, which is common on Kosrae, though it is threatened and in decline on Pohnpei (Lewis 2008). *Ponapea hosinoi* has a very small natural range on Pohnpei making it highly vulnerable to habitat loss. *Ponapea palauensis* is considered Critically Endangered under IUCN red listing criteria (Costion et al. 2009) with only two small populations remaining. *Clinostigma* is a genus of 11 species endemic to the south and western Pacific. One species, *C. ponapense*, is endemic to Pohnpei where it is abundant in some localities, while the other, *C. carolinense*, is endemic to Chuuk. The genus *Hydriastele* was recently revised to incorporate three other genera including *Gulubia*. Its range now stretches from New Zealand to Indonesia and the Pacific with most species occurring in New Guinea. The Palau species is found in patches scattered throughout the Rock Islands. *Metroxylon* is the sago palm genus, widely utilized for the starch extracted from the pith. There are seven species total, the Micronesian species being the only species that is not monocarpic (flowers only once then dies).

Clinostigma carolinense (Becc.) Moore & Fosberg	Chuuk	--	--	--
Clinostigma ponapense (Becc.) Moore & Fosberg	Pohnpei	V	T	--
Hydriastele palauensis (Becc.) W.J.Baker & Loo	Palau	L	T	U-R
Metroxylon amicarum (H.Wendl.) Hook.f.	Micronesia	--	T	--
Ponapea hosinoi Kaneh.	Pohnpei	V	T	--
Ponapea ledermanniana Becc.	E. Carolines	V	T	--
Ponapea palauensis Kaneh.	Palau	L	T	R

CYPERACEAE
13/64(4)

There are over 4,000 species of sedges found worldwide. They are most abundant in the tropics and most commonly associated with wetland or riparian areas and poor soils. They are well represented in Micronesia where there is no shortage of poor soils and wet areas. Four species are considered endemic.

Hypolytrum dissitiflorum Steud.	E. Carolines	--	H	--
Hypolytrum flavinux (T. Koyama) D.A. Simpson	Palau	V	H	--
Fimbristylis palauensis Ohwi	Palau	V	H	--
Mapania pacifica (Hosok.) T. Koyama	E. Carolines	V	H	--

HEMEROCALLIDACEAE
1/2(2)

This family has tentatively been placed within the Xanthorrhoeaceae as a subfamily along with Asphlodaceae by some authors. Since morphological support for this view is lacking and molecular data remain inconclusive we retain it as a distinct family following Mabberley (2008). Xanthorrhoeaceae sensu stricto are the characteristic “grass trees” endemic to Australia forming a monotypic family of approximately 28 species. Hemerocallidaceae has approximately 63-85 species distributed on all continents except North America. *Dianella* has about 40 known species, many of which are endemic to Australia. The two Micronesian species commonly occur in open savannahs or barren volcanic soils. They have attractive blue to purplish flowers and fruits making them good native ornamental candidates.

Dianella carolinensis Laut.	W. Carolines	V	H	C
Dianella saffordiana Fosberg & Sachet	Guam	V	H	C

ORCHIDACEAE
50/120(85)

The orchids form the largest angiosperm family with over 22,000 species worldwide. It is the most diverse family in Micronesia for both native and endemic species and also one of the most likely Micronesian plant groups to have new species yet to be discovered. There is a long list of potential new orchid species from Micronesia. These tentative names are not included here as most are unverified records or based on infertile specimens. The three largest orchid genera in Micronesia are *Bulbophyllum* (6), *Phreatia* (7), and *Dendrobium* (12). *Bulbophyllum* is the largest orchid genus and with over 1,800 species is one of the largest plant genera in the world. Its centre of diversity is New Guinea. *Phreatia* is a small genus of about 150 mostly Indomalesian species. Some were formerly placed in *Rhynchophreatia,* which is no longer an accepted genus. *Dendrobium* is also a large genus found from Asia to the Pacific. All are either epiphytes or lithophytes. Most of

Micronesia’s orchids have small inconspicuous flowers, though a few such as *Dendrobium palawense*, *Dendrobium mirbelianum*, and *Dipodium freycinetioides* have much horticultural potential and are already being harvested in alarming quantities from the forests for local gardens.

Aglossorrhyncha micronesiaca Schltr.	Palau	V	E	--
Agrostophyllum kusaiense Tuyama	Kosrae	V	E	--
Agrostophyllum palawense Schltr.	Palau	V	E	--
Bulbophyllum desmanthum Tuyama	Palau	V	E	--
Bulbophyllum fukuyamae Tuyama	Kosrae	V	E	--
Bulbophyllum guamense Ames	Guam	--	E	--
Bulbophyllum hatusimanum Tuyama	Palau	V	E	--
Bulbophyllum kusaiense Tuyama	Kosrae	V	E	--
Bulbophyllum micronesiacum Schltr.	Micronesia	V	E	--
Cherostylis raymundii Schltr.	W. Carolines	--	H	R
Chiloschista loheri Schltr.	Palau	G	E	C
Cleisostoma porrigens (Fukuy.) Garay	Palau	V	E	U
Coelogyne guamensis Ames.	Micronesia	V	H-E	--
Corybas ponapensis Hosok. & Fukuy.	Pohnpei	V	E	R
Crepidium calcarea (Schltr.) D. L. Szlachetko	Palau	L	H	--
Crepidium kerstingiana (Schltr.) D.L. Szlachetko	Palau	G	H	U
Crepidium palawensis (Schltr.) D. L. Szlachetko	Palau	V	H	U
Crepidium setipes (Schltr.) D. L. Szlachetko	Palau	V	H	A
Cystorchis ogurae (Tuyama) Ormerod & P.J.Cribb	Palau	V	H	--
Dendrobium adamsii A. D. Hawkes	Pohnpei	V	E	--
Dendrobium brachyanthum Schltr.	Palau	V	E	C
Dendrobium carolinense Schltr.	E. Carolines	V	E	C
Dendrobium guamense Ames.	S. Marianas	--	E	--
Dendrobium implicatum Fukuy.	Palau	V	E	--
Dendrobium kerstingianum Schltr.	Palau	V	E	--
Dendrobium kraemeri Schltr.	Carolines	G	E	--
Dendrobium oblongimentum Hosok. & Fukuy.	S. Marianas	--	E	--
Dendrobium okabeanum Tuyama	Chuuk	--	E	--
Dendrobium palawense Schltr.	Palau	L	E	--
Dendrobium patentifiliforme Hosok.	Palau	V	E	--
Dendrobium ponapense Schltr.	E. Carolines	--	E	--
Didymoplexis trukensis Tuyama	Chuuk	--	H	--
Dienia volkensii M.A. Clem. & D.L. Jones	W. Carolines	V	H	--
Diplocaulobium carolinense A. D. Hawkes	Pohnpei	V	E	--
Diplocaulobium elongaticolle (Schltr.) Hawkes	W. Carolines	G	E	C
Diplocaulobium flavicolle (Schltr.) Hawkes	Pohnpei	V	E	--
Dipodium freycinetioides Fukuy.	Palau	V	E	--
Glomera carolinensis L. O. Williams	Pohnpei	V	E	--
Liparis dolichostachya Fukuy.	Palau	V	H-E	--
Liparis palawensis Tuyama	Palau	V	H-E	--
Liparis yamadae (Tuyama) Fosberg & Sachet	Palau	V	H-E	--

Malaxis alamaganensis S. Kobay.	N. Marianas	V	H	R
Malaxis trukensis (Fukuy.) Fosberg & Sachet	Chuuk	--	H	--
Micropera draco (Tuyama) P.J. Cribb & Ormerod	Palau	V	E	--
Microtatorchis hosokawae Fukuy.	Pohnpei	V	E	--
Moerenhoutia hosokawae (Fukuy.) Tuyama	Carolines	V	H	--
Moerenhoutia laxa Schltr.	Palau	V	H	U
Moerenhoutia leucantha Schltr.	Ponhpei	V	H	--
Nervilia jacksoniae Rinehart & Fosberg	Marianas	--	H	--
Nervilia palawensis Schltr.	W. Carolines	G	H	R
Nervilia trichophylla Fukuy.	Palau	V	H	R
Oberonia hosokawae Fukuy.	Ponhpei	V	E	--
Oberonia palawensis Schltr.	Palau	G	E	--
Oberonia ponapensis Tuyama	Pohnpei	V	E	--
Oberonia rotunda Hosok.	W. Carolines	V	E	--
Peristylus carolinensis (Schltr.) Tuyama	Pohnpei	V	H	--
Peristylus palawensis (Tuyama) Tuyama	Palau	V	H	R
Peristylus setifera Tuyama	W. Carolines	V	H	R
Phreatia carolinensis Schltr.	Pohnpei	V	E	--
Phreatia kanehirae Fukuy.	Palau	V	E	--
Phreatia kusaiensis Tuyama	Kosrae	V	E	--
Phreatia palawensis (Schltr.) Tuayama	Palau	L	E	--
Phreatia ponapensis Schltr.	Pohnpei	V	E	--
Phreatia pseudothompsonii Tuyama	Ponhpei	V	E	--
Phreatia thompsonii Ames	Micronesia	--	E	--
Pseuderia micronesiaca Schltr.	Carolines	V	E	--
Pseudovanilla ponapensis (Kaneh. & Yam.) Garay	Pohnpei	V	E-V	U
Rhynchophreatia pacifica Fukuy.	Kosrae	V	E	--
Robiquetia kusaiensis Fukuy.	Kosrae	V	E	--
Robiquetia lutea (Volk.) Schltr.	Carolines	--	E	--
Robiquetia palawensis Tuyama	Palau	G	E	--
Robiquetia trukensis Tuyama	Chuuk	V	E	--
Spathoglottis carolinensis Schltr.	W. Carolines	V	H	--
Spathoglottis micronesiaca Schltr.	W. Carolines	V	H	--
Taeniophyllum marianense Schltr.	Carolines	--	E	--
Taeniophyllum palawense Schltr.	Palau	V	E	--
Taeniophyllum petrophilum Schltr.	Carolines	--	E	--
Taeniophyllum trukense Fukuy.	Chuuk	--	E	--
Thrixspermum arachnitiforme Schltr.	Ponhpei	V	E	--
Thrixspermum ponapense Tuyama	Pohnpei	V	E	--
Trichoglottis ledermannii Schltr.	Carolines	G	E	--
Vrydagzynea micronesiaca Schltr.	Carolines	V	H	--
Zeuxine fritzii Schltr.	Micronesia	--	H	--
Zeuxine ovata (Gaudich.) Garay. & W. Kittr.	Marianas	--	H	--
Zeuxine palawensis Tuyama	Palau	V	H	C

PANDANACEAE

2/17(12)

Pandanaceae, the screwpine family, is a large Old World family of over 800 species occurring from tropical Africa and Madagascar to the Pacific. *Freycinetia* is a genus of woody climbers. They are easy to distinguish in a dense forest canopy by their trifarious spiraled leaves. Micronesia has three species, two of which are endemic. The third, *F. reineckei*, also occurrs in Samoa. *Pandanus* is a large genus, which has been subject to considerable taxonomic dispute in the Pacific due to some species such as *P. tectorius* having variable forms from island to island. These plants do well along the coast and in poor soils but seem to occur in just about every habitat in Micronesia from the fire adapted *P. tectorius* association in the savannahs to the salt tolerant *P. kanehirae* swamp forest association of Palau. They also range considerably in size from the enormous *P. dubius* to small understory trees such as *P. amiriikensis,* and even potentially small scandent shrubs as observed for the elusive *P. peiliuensis*. All parts of the plants are widely utilized by Micronesians for food, basketry, mats, clothing, medicine, fishing tools, and even sails.

Freycinetia ponapensis Martelli	E. Carolines	V	WL	--
Freycinetia villalobosii Martelli	Palau	V	WL	C-A
Pandanus aimiriikensis Martelli	Palau	V	T(u)	C-A
Pandanus amissus Huynh	Kosrae	V	T	U
Pandanus japensis Martelli	Yap	--	T	--
Pandanus kanehirae Martelli	Palau	V	T	U
Pandanus kusaicolus Kaneh.	Kosrae	V	T	U
Pandanus lorencei Huynh	Palau	L	T	--
Pandanus macrojeanneretia Martelli	Palau	V	T	U
Pandanus palawensis Martelli	Palau	V	T	--
Pandanus patina Martelli	Pohnpei	V	T-S	--
Pandanus peliliuensis Kaneh.	Palau	L	T-S	R

POACEAE

46/90(7)

The grass family is one of the few angiosperm families that is literally global in distribution. Over 10,000 species of grasses are found from the arctic to sub-Saharan Africa and into the Pacific, and the family is subdivided into 13 subfamilies and over 650 genera. The adaptability and evolutionary capacity of grasses is evident even in Micronesia’s Gilbert Islands. *Lepturus pilgerianus* is the only endemic plant species that occurs on these small atolls dominant with the characteristic Pacific atoll vegetation. Despite the reputation of many grass species as weeds, including species in the genera *Digitaria, Isachne, Ischaemum, Panicum,* and *Sporobolus,* there are also both native and endemic species in Micronesia. The grasses are one of the most important plant families to human society, having given rise to most major cereal crops. They were not exploited for food by the islanders of Micronesia in the pre-European contact era, though today rice is a common staple and in many islands has almost entirely replaced traditional staples.

Digitaria gaudichaudii (Kunth) Henrard	Marianas	--	H	--
Digitaria mezii Kaneh.	Marianas	--	H	--
Isachne carolinensis Ohwi	Pohnpei	V	H	--
Ischaemum longisetum Merrill	Marianas	L	H	--
Lepturus pilgerianus Hans. & Potzt.	Gilbert Is.	L	H	--
Panicum palauense Ohwi	Palau	V	H	--
Sporobolus farinosus Hosok.	Micronesia	L?	H	--

POTAMOGETONACEAE

2/3(1)

The pondweed family is comprised of about 120 species worldwide. They are all aquatic perennial herbs with tetramerous flowers lacking petals. Many species are regarded as having vitally important roles in their ecosystems by providing habitat and food for other organisms, notably ducks. The Marianas endemic *Potamogeton* species may have been a food plant for the Marianas mallard (Stone 1970), *Anas oustaleti*, which was declared extinct in 1981 after several decades of decline from loss of wetland habitat.

Potamogeton marianensis Cham. & Schltdl.	Guam	A	H	--

ZINGIBERACEAE

4/6(1)

Alpinia is the largest and most widespread genus in the ginger family. It has approximately 230 species distributed in the Asia-Pacific region, though recent studies indicate that it is a polyphyletic genus (Kress et al. 2005). *Alpinia carolinensis* belongs to subgenus *Dieramalpinia* (Smith 1990), which is comprised of taxa occurring mostly east of Wallace’s Line. Many species of *Alpinia* are popular as ornamentals. Micronesia’s endemic, “giant ginger” has for the most part, not been exploited in this regard though many plant enthusiasts express utter amazement at its size. It is one of the largest species in the entire ginger family, reaching up to 8 meters (26 feet) tall. It is a common component of the forest understory on the volcanic islands.

Alpinia carolinensis Koidz.	Carolines	V	H/T	C

EUDICOTS

(195)

ACANTHACEAE

5/8(3)

Acanthaceae is a mostly tropical family of about 4,000 species. They are often easily identified by their opposite leaves with swollen nodes and showy petalaoid bracts, but not all species display these characters. There are three native and one endemic *Hemigraphis* species in Micronesia, occurring as small herbs. The endemic *H. pacifica* is poorly known, though has been observed and collected along the stream banks of Babeldaob. It has been confused with *H. palauana,* which Fosberg et al. (1979) treat as a synonym for *H. angustifolia*, native to Palau. *Pseuderanthemum* has several ornamental species that are widely cultivated and popular in Micronesia. Fosberg and Sachet (1980) described an additional endemic *Pseuderanthemum* distinct from *P. inclusum* by its leaf and inflorescence shape, longer floral parts, and warty seeds.

Hemigraphis pacifica Hosok.	Palau	V	H	--
Pseuderanthemum inclusum Hosok.	Palau	V	H	--
Pseuderanthemum palauense Fosberg & Sachet	Palau	G	H	--

ANACARDIACEAE
5/7(4)

The Anacardiaceae family has about 600 species with its center of diversity in Malesia. The family contains the well-known cash crops mango, cashew, and the poison ivy of North America. Members of this family contain highly poisonous sap that often turns black and is caustic, causing minor to severe skin irritations. A liberal dose of *Semecarpus* sap in particular can lead to hospitalization. Micronesians take care when entering the forest, especially after rain, and avoid this plant entirely. A fleshy receptacle subtends the fruits, which is allegedly edible. The genus has about 60 species, mostly in Southeast Asia. *Buchanania* is a small genus of roughly 25 tree species from Asia to the Pacific. The two endemics from the Western Carolines are difficult to distinguish and have been confused in Palau. They may be separated by preferred habitat. *B. palawensis* is only found in the limestone forests and coastal habitats of Palau and is uncommon (Kitalong et al. 2008). *B. engleriana* occurs abundantly in the volcanic soils of Babeldaob in addition to Yap.

Buchanania engleriana Volk.	W. Carolines	V	T	C
Buchanania palawensis Lauterb.	Palau	L	T	U
Semecarpus kraemeri Lauterb.	Chuuk	--	T	--
Semecarpus venenosus Volk.	W. Carolines	G	T	C

APOCYNACEAE
14/21(7)

The Apocynaceae family now incorporates the former family Asclepiadaceae as a subfamily. Asclepiadaceae was split from Apocynaceae in the 1800's primarily on the basis of the presence of pollinia. A pollinium is a sac of pollen grains that is dispersed by sticking to an insect as it visits the flower for nectar. Orchids have also independently evolved this unique pollination strategy. Molecular data now show that Asclepiadaceae is not monophyletic and is nested within Apocynaceae. The family is easy to identify by its milky white latex, opposite or whorled leaves, and often two-parted fruits. The latex is often highly toxic and for some species it is known to cause temporary to permanent blindness. Thus care should be taken when handling the plants. *Rauvolfia,* a genus of about 110 mostly tropical trees and shrubs, is of interest for research in medicinal plants. Several members of this genus are rich in biochemical compounds that have been used in medicine, notably *R. serpentina*, which has been used to treat snake bites and wounds for millennia and more recently as the source of reserpine, an antihypertensive drug and tranquilizer.

Hoya schneei Schltr.	Pohnpei	V	HV	--
Hoya trukensis Hosok.	Chuuk	--	HV	--
Lepinia ponapensis Hosok.	Pohnpei	V	T	RR
Lepiniopsis trilocularis Mgf.	Carolines	L	T-S	--
Melodinus insularis (Markgr.) Fosberg	Palau	V	WL	--
Ochrosia mariannensis A.DC.	Marianas	G	T	C
Rauvolfia insularis Markgr.	Palau	V	T	U,RR

APTANDRACEAE

1/1(1)

Aptandraceae is a very small family of parasitic plants. There are only 34 species but these are subdivided into eight different genera. *Anacalosa* was formerly placed in the Olacaceae family. *Anacalosa* is a pantropical genus with about 18 species. The plants are dioecious with leaves two-ranked on zigzag shaped branches. *Anacalosa glochidiiformis* is a small tree with small white flowers and orange fruits. The members of this family are suspected to be root parasites; however, direct evidence of functional haustoria, the roots that penetrate the host's tissue to extract nutrients, has yet to be recorded.

Anacalosa glochidiiformis Kaneh. & Hatus.	Palau	G	T	U

AQUIFOLIACEAE

1/1(1)

The genus *Ilex*, comprises the entire montypic Aquifoliaceae family, commonly known as the hollies. There are over 400 species found worldwide. The genus is most diverse in the tropics but also extends into temperate regions. Many are endemic to mountain ranges in the temperate tropical montane flora, but species also occur in the humid lowlands and on oceanic islands. *Ilex volkensiana* is found only in the cloud forests of Pohnpei.

Ilex volkensiana (Loes.) Kaneh. & Hatus.	Pohnpei	V	T	--

ARALIACEAE

3/9(8)

The Araliaceae or ginseng family is a mostly tropical family occurring worldwide. *Osmoxylon* has approximately 60 species, mostly concentrated in east Malesia, the Philippines, and Melanesia. Its Pacific distribution is limited to the Solomon Islands, Vanuatu, and Micronesia. *Osmoxylon oliveri* is a common understory component throughout Palau, whereas *O. pachyphyllum* is less common but widespread, and *O. truncatum* is only known from a few collections. It is considered endemic to southern Babeldaob. *Osmoxylon mariannense* is endemic to Rota. *Polyscias* is a genus of small to medium sized understory trees in the tropics with roughly 130 species. Molecular work (Plunkett et al. 2001) suggests the genus is paraphyletic with at least four to five distinct clades represented in the Pacific. *Schefflera* is a polyphyletic genus of over 600 species, also with 5 separate geographically distinct clades (Plunkett 2005). Micronesia's native *S. elliptica* belongs to the Asian clade. However the Chuuk endemic *S. kraemeri* has not been included in any molecular phylogenies to date. This is worth noting considering a separate Pacifc clade of *Schefflera* is recognized with its center of diversity in Melanesia. Thus, Micronesia's *Schefflera* and *Polyscias* species could potentially be derived from more than one dispersal event within each genus. The Melanesian-centered clade of *Schefflera* is sister to *Meryta*. *Meryta* is a genus of approximately 30 species endemic to the South Pacific, all restricted to islands or island groups from New Caledonia to the Marquesas (Tronchet 2005).

Osmoxylon mariannense Fosberg & Sachet	S. Marianas	--	T	--
Osmoxylon oliveri Fosberg & Sachet	Palau	G	T(u)	A
Osmoxylon pachyphyllum Fosberg & Sachet	Palau	G	T(u)	U
Osmoxylon truncatum (Kaneh.) Fosberg & Sachet	Palau	V	T(u)	--
Meryta senfftiana Volkens	Micronesia	--	T	C
Polyscias grandifolia Volkens	Micronesia	L	T(u)	C
Polyscias subcapitata Kaneh.	Kosrae	V	T	--
Schefflera kraemeri Harms	Chuuk	--	--	--

BORAGINACEAE
4/8(1)

Cordia is a pantropical genus with over 200 species worldwide. Its center of diversity is in the West Indies. The borage family is famous in botany for the *Echium* species of the Canary Islands that show an insular shift to woodiness from an herbaceous lineage. The borage family has adapted well to insular life and is represented in Pacific atoll vegetation with widespread *Heliotropium, Cordia,* and *Tournefortia* species. *Cordia micronesica* is likely derived from the widespread palaeotropic species *C. subcordata*, characteristic of strand vegetation. Both its flowers and fruits are substantially smaller than the latter, however, and its leaves are more distinctly serrated. *Cordia subcordata* is revered by islanders for its lightweight durable wood but also has many other uses including dye and medicine.

Cordia micronesica Kaneh. & Hatus.	Palau	V	T	U-R

CAPPARACEAE
2/3(1)

The relatively small caper family is closely related to Brassicaceae, the mustard family. *Capparis* has about 250 species worldwide of mostly shrubs or lianas and is famous for the pickled condiments capers. *Capparis carolinensis* occurs on the limestone islands of Palau. It was treated as a synonym by Jacobs (1960) but was confused with its relative and putative ancestor, *C. cordifolia*. *Capparis carolinensis* has larger, more elliptic leaves compared to *C. cordifolia*'s distinct orbicular leaves and has smaller, more numerous, clustered flower buds. *Capparis cordifolia* has a more widespread distribution in the Pacific but in Micronesia occurs only on Palau's limestone islands.

Capparis carolinensis Kaneh.	Palau	L	S	--

CELASTRACEAE
3/5(2)

The Celastraceae family has approximately 1,350 species worldwide and now incorporates the former Hippocrateaceae. They most commonly occur as small trees, shrubs, or lianas, but there are two herbaceous genera. The distinctive nectar disk present in the flowers often characterizes them. In most species, the flowers are yellow to greenish and inconspicuous. The family as a whole is not very economically important, though a few species are used as ornamentals in the genera *Celastrus* and *Euonymus,* and a narcotic is derived from *Catha edulis*, a native of East Africa and Arabia. *Maytenus* is a pantropical genus with 200-270 species. Both of Micronesia's endemics are relatively common where they occur.

Maytenus palauica (Loes.) Fosberg	Palau	G	S	C
Maytenus thompsonii (Merr.) Fosberg	S. Marianas	L	S	C

CLUSIACEAE
4/10(7)

The Clusiaceae (or Guttiferae) is a small family of about 600 species mostly restricted to the moist tropics. Members of this family have opposite leaves and usually have latex that can be creamy to off white or bright yellow to orange in color. *Garcinia* is the mangosteen genus, named after the esteemed fruit from Southeast Asia, *G. mangostana*. Several other species are also cultivated for their fruits, and others have medicinal compounds that are utilized in traditional and modern medicine. *Garcinia* now includes the genus *Pentaphalangium,* which was formerly applied to *G. carolinensis* and *G. volkensii*. The genus *Calophyllum* is well known in the Pacific from the widespread strand tree *Calophyllum inophyllum*. This has evolved into a separate variety, *C. inophyllum* var. *wakamatsui*, found inland from the coasts on the volcanic island of Babeldaob where it can reach impressive sizes along ridgelines. Palau's other endemic, *C. pelewense,* is probably derived from *C. soulattri,* which is very similar in morphology. *Calophyllum soulattri* is also widespread in distribution from Vietnam to Australia. *Kayea* is a smaller genus of about 65 species from India to Australia. The Palau endemic is an uncommon riparian tree with foliage resembling *Cynometra ramiflora,* and thus the same vernacular name is sometimes applied to both.

Calophyllum pelewense P.F. Stevens	Palau	V	T(c)	U
Garcinia carolinensis (Ltb.) Kosterm.	Chuuk	--	T	--
Garcinia matsudai Kaneh.	Palau	V	T	C-A
Garcinia ponapensis Laut.	E. Carolines	V	T	--

Garcinia rumiyo Kaneh.	W. Carolines	--	T	--
Garcinia volkensii (Ltb.) Kosterm.	Yap	--	T	--
Kayea pacifica Hosok.	Palau	V	T	U

COMBRETACEAE

3/7(3)

The Combretaceae family consists of about 500 species of trees or lianas mostly in the tropics. Species of *Terminalia* are generally large trees with a characteristic "pagoda-like" branching pattern and leaves clustered at the twig tips in rosettes. Its name is derived from the Latin *terminus*, referring to the terminal foliage and branching pattern. *Terminalia carolinensis* is a large buttressed tree found in the swamp forests of Kosrae and Pohnpei. *Terminalia crassipes* is a large riparian tree only known from two river systems in Palau. *Terminalia rostrata*, also a large tree, is only known from the tiny, 7.3 km², uninhabited Asuncion Island.

Terminalia carolinensis Kaneh.	E. Carolines	V	T(c)	--
Terminalia crassipes Kaneh. & Hatus.	Palau	V	T(c)	R, RR
Terminalia rostrata Fosberg & Falanruw	N. Marianas	V	T(c)	R

CUCURBITACEAE

2/3(1)

The Cucurbitaceae family has about 845 mostly vine or liana species worldwide and can easily be recognized by the hairy palmate leaves and branched tendrils occurring at a 90° angle with the leaf petiole at the nodes. There are numerous economically important crops in this family, many of which are cultivated in Micronesia including melons, squashes, and cucumbers. There are only a few native species. *Trichosanthes* is one of the largest genera with about 100 species, mostly occurring in Australasia. The only record of *T. hosokawae* we are aware of is Fosberg's type collection from the limestone Rock Island of Aulupse'el. It likely occurs throughout the Rock Islands, though Fosberg noted that it was rare.

Trichosanthes hosokawae Fosberg	Palau	L	WL	--

ELAEOCARPACEAE

1/6(6)

Elaeocarpaceae is a tropical family of trees and shrubs with a classic Gondwanan distribution of extant taxa. There are over 600 species, over half of which are within the largest genus, *Elaeocarpus.* They are easily recognized by the foliage. The leaves are often serrated with a swollen petiole, sometimes have domatia, and nearly always turn yellow to red before falling to the ground. The flowers are also very distinctive, usually with fringed petals. This genus has many endemic species with narrow ranges. The center of diversity is in Southeast Asia, 60 species are endemic to Papuasia (New Guinea to

Solomon Islands), and new species are still being described in Australia where the flora is well known. All Micronesian *Elaeocarpus* species are considered endemic. It is worth noting that although the Palau population of *E. joga* occurs abundantly on the volcanic island of Babeldaob, the Marianas populations are only known from limestone based soils and have been shown to be in decline (Ritter & Naugle 1999).

Elaeocarpus carolinensis Koidz.	E. Carolines	V	T	--
Elaeocarpus joga Merr.	Micronesia	G	T	--
Elaeocarpus kerstingianus Schltr.	Pohnpei	V	T	--
Elaeocarpus kusaiensis Kaneh.	E. Carolines	V	T	--
Elaeocarpus kusanoi Kaneh.	E. Carolines	V	T	--
Elaeocarpus rubidus Kaneh.	Palau	L	T	--

ERICACEAE
1/1(1)

The following species was formerly placed in Epacridaceae and was transferred from the genus *Styphelia* or *Cyathodes* to *Leptecophylla* along with six other species from New Guinea and the Pacific (Weiller 1999). Epacridaceae were formerly understood as closely related to Ericaceae but as a separate Gondwanan family. They now form the subfamily Styphelioideae within Ericaceae. Most species occur in Australia and New Zealand, but they also occur from Southeast Asia into the Pacific (Hawaii and the Marquesas) and the southern tip of South America. Ericaceae species prefer poor, acidic soils and temperate climates. Tropical members of the family rarely occur in the lowlands. *Leptecophylla mariannensis* is only known from Alamagan, an eleven square kilometer island located north of Saipan. The island is volcanic with a large caldera at the summit and reaches to 744 meters in elevation. *Leptecophylla mariannensis* occurs near the caldera up to about 700 meters (Sleumer 1963).

Leptecophylla mariannensis (Kaneh.) C.M.Weiller	N. Marianas	V	S	RR

EUPHORBIACEAE
12/21(8)

Euphorbiaceae, the spurge family, used to include what are now Phyllanthaceae and Putranjavaceae. It is a large family of nearly 6,000 species with its center of diversity in the Indomalayan tropics. There are few universal vegetative characters for this family but the plants often have leaves of irregular size with glands near or at the base or petiole and/or with stipules present. The flowers are unisexual and the fruits are nearly always three-parted. *Claoxylon* has about 80 species distributed from Madagascar to the Pacific. The flowers are very small and inconspicuous born on spikes in the axils of the leaves. *Croton* is a large pantropical genus with about 1300 species. A number of species are used for traditional medicine, food, and even research for potential biofuels. *Croton saipanensis* is only known from Saipan. *Euphorbia* is one of the largest genera of flowering plants. Most species are succulent or xerophytic and have toxic white latex. There are a number of weedy *Euphorbia* species in Micronesia. The native ones, including the endemic *E. gaudichaudii,* tend to be small herbs or shrubby strand plants. *Macaranga* is a palaeotropic genus of about 240 species. They are often colonizers found in disturbed sites or primary vegetation, and many species have been documented to have symbiotic relationships with ants that live in the hollow stems.

Claoxylon carolinianum Pax & Hoffm.	Pohnpei	V	T	--
Claoxylon longiracemosum Hosok.	Palau	V	T	U
Claoxylon marianum Mueller-Argoviensis	S. Marianas	L	T-S	C
Cleidion sessile Kaneh. & Hatus.	Palau	L	T	--
Croton ripensis Kaneh. & Hatus.	Pohnpei	V	T-S	R
Croton saipanensis (Hosok.) Hosok.	S. Marianas	--	--	--
Euphorbia gaudichaudii Boissier	Micronesia	L,V	S	--
Macaranga thompsonii Merr.	Marianas	L	T-S	C

FABACEAE
27/46(12)

The legume family is the third largest family of flowering plants with approximately 19,400 species worldwide. They are easy to distinguish, having alternate, usually compound leaves with stipules and fruits usually as legumes. Fabaceae is a very economically important family with many crops and nitrogen fixing plants. Although there are numerous introduced and weedy Fabaceae species present in Micronesia, there are also a number of endemics with very narrow ranges. Both species of *Parkia* have very small population sizes and are single island endemics. *Serianthes nelsonii* is endemic to the islands of Guam and Rota. There is only one known mature tree left on Guam (Stone 1970; Wiles 1998). The population on Rota is more intact with about 120 trees, though it is expected to decline from lack of regeneration (Wiles 1998). *Parkia parvifoliola* qualifies for Endangered status under the IUCN red listing criteria (Costion et al 2009) and *Serianthes nelsonnii* is listed as Critically Endangered (Wiles 1998). *Mucuna pacifica* and *Rhynchosia calosperma* are only known from Saipan, Tinian, and Rota, and *Derris mariannensis* is only known from the island of Rota. *Tephrosia mariana* is endemic to the Micronesia bioregion but only known from Guam and Chuuk.

Canavalia megalantha Merr.	Marianas	--	WL	--
Crudia cynometroides Hosok.	Palau	V	T	U
Cynometra yokotai Kaneh.	Chuuk	--	T	--
Dalbergia hosokawae (Hosok.) Costion & Lorence	Palau	V	WL	--
Dalbergia palauensis Hosok.	Palau	V	WL	--
Derris mariannensis Hosok.	S. Marianas	--	WL	--
Mucuna pacifica Hosok.	S. Marianas	--	--	--
Parkia korom Kaneh.	Pohnpei	V	T	R
Parkia parvifoliola Hosok.	Palau	V	T(c)	RR
Rhynchosia calosperma Warb.	S. Marianas	--	--	--
Serianthes nelsonii Merr.	S. Marianas	--	T	R
Tephrosia mariana DC. & Hosok.	Micronesia	--	S	--

GENTIANACEAE

1/2(1)

Gentianaceae is a cosmopolitan family with over 1,600 species occurring worldwide, mainly in temperate regions. Their foliage is distinctive in having opposite leaves with the two petioles joining at the base. *Fagraea* is a genus of about 75 species, one of which is now a popular ornamental in the Pacific, particularly in Hawaii. *Fagraea berteroana* is native to Australia, New Guinea, Micronesia, and east to the Marquesas. The Palau endemic *F. ksid* is very close to *F. berteroana* in its morphology and may be derived from it. It is easily distinguished from the latter by its elongated ovoid fruit and larger flowers with stamens and style that are not exserted. *Fagraea berteroana* in Palau also tends to occur as an epiphyte in the forest while *F. ksid* occurs as a tree in the savannas or savanna edges and along ridgelines.

Fagraea ksid Gilg & Gilg-Ben.	Palau	V	T	C

GESNERIACEAE

1/4(4)

Gesneriaceae is almost entirely tropical and is close to Lamiaceae, the mint family. All species are either herbaceous or soft-stemmed trees or shrubs. They have opposite serrated leaves often with soft hairs or pubescence and flowers with bilateral symmetry. The genus *Cyrtandra* has radiated substantially throughout the Pacific with a high percentage of single island endemics. It has nearly 600 known species and is most diverse in Southeast Asia. Recent molecular work strongly suggests that the species in the Pacific are Southeast Asian derived and have radiated from a single dispersion event followed by stepping stone migration across the Pacific (Cronk et al. 2005). Micronesia has four species, and all are endemic with limited distributions.

Cyrtandra kusaimontana Hosok.	Kosrae	V	--	U-R
Cyrtandra palawensis Schltr.	Palau	V	WL	U-C
Cyrtandra todaiensis Kaneh.	Palau	L	S	--
Cyrtandra urvillei C.B. Cl.	E. Carolines	V	--	U

LAMIACEAE

8/16(1)

The mint family was recently expanded to include many, but not all, previous members of Verbenaceae. It has worldwide distribution with many important economic plants, particularly herbs and spices. Plants in this family often have aromatic leaves, square shaped stems, and bi-symmetric flowers with an upper and lower lip, and branches of woody species often have distinct lenticels. *Callicarpa*, a genus of up to 140 recognized species, was formerly placed in Verbenaceae. It has global distribution, but most species occur in East and Southeast Asia. There is very little information available on *C. lamii*. It even escaped Stone's (1970) attention in the Flora of Guam, and thus it is probably very similar to the widespread *C. candicans*. Fosberg & Sachet (1980) also noted that it was only weakly distinct from *C. candicans*, and that the varieties of the latter species they recognized and its relationships with other Indopacific species are also unclear requiring further study. Kawakubo (1986) also noted a high degree of morphological variation in endemic *Callicarpa* of the Bonin Islands. Molecular studies may revise species concepts in this genus. *Callicarpa* remains unplaced within the Lamiaceae.

Callicarpa lamii Hosok.	Marianas	--	S	--

MALVACEAE
18/23(6)

The Malvaceae family now includes Tiliaceae, Sterculiaceae, and Bombacaceae as subfamilies in a larger family concept, Malvaceae sensu lato, which includes over 4,000 species. The family can often be recognized without fertile material by its alternate stipulate leaves, palmate venation or palmately compound leaflets, and stellate hairs on the leaves. The branches often have “strong” or very fibrous bark that peels down the branch instead of breaking clean, often with mucilage. *Hibiscus tiliaceus*, a common Pacific strand and wetland plant, is exploited for just these characters. Long strips of bark are used to extract the juice of sakau in Pohnpei, giving it the characteristic slimy texture. Other important economic plants in this family include cotton and chocolate. Micronesia’s endemics range from canopy trees to pioneer shrubs. *Heritiera longipetiolata* occurs rooted in crevices in dissected limestone slopes and plateaus in the Marianas. It is listed as Vulnerable on IUCN Red List and known outside the Marianas only from Pohnpei. *Sterculia* is a pantropical genus of 150 species. *Sterculia palauensis* is a large buttressed tree only found on Palau’s limestone islands, and *S. ponapensis* is known only from Pohnpei and Yap. *Trichospermum* is predominantly a Malesian genus with its diversity centered in New Guinea. Two species occur in Micronesia, and are both are endemic. They are common shrubs occurring in primary vegetation or at edges of savannahs.

Heritiera longipetiolata Kaneh.	Micronesia	L	T	R
Melochia villosissima Merr.	Micronesia	V	S	U
Sterculia palauensis Kaneh.	Palau	L	T(c)	--
Sterculia ponapensis Kaneh.	Carolines	V	T	--
Trichospermum ikutai Kaneh.	Yap	--	S	--
Trichospermum ledermannii Burret	Palau	V	S	A

MELASTOMATACEAE
3/8(6)

The Melestomataceae family is a large pantropical to substropical family with over 5,000 species. The center of diversity is in the neotropics. Members of this family are easy to distinguish by their opposite leaves with three or more conspicuous veins ascending from the base with tertiary veins occurring perpendicular to the midrib. The flowers are also distinct in having porose anthers with conspicuous connectives or appendages. *Astronidium* has 70 species from Indomalesia to the Pacific. Three are endemic in Micronesia: *Astronidium kusaianum* was reduced to synonymy under *A. carolinense*.

Medinilla is a palaeotropic genus of shrubs and lianas. In Micronesia the three endemics species occur as lianas or climbing shrubs.

Astronidium carolinense (Kaneh.) Markgr.	Chuuk	--	T	--
Astronidium palauense (Kaneh.) Markgr.	Palau	V	T(u)	C
Astronidium ponapense (Kaneh.) Markgr.	Pohnpei	V	T	--
Medinilla blumeana Mansf.	Palau	V	WL	--
Medinella diversifolia Kaneh.	Kosrae	V	WL	RR
Medinilla medinilliana (Gaud.) Fosberg & Sachet	Marianas	--	S-WL	C

MELIACEAE
4/5(1)

Meliaceae, the mahogany family, is a pantropical family with over 600 species. Mahogany is native to Central and South America, but it is widely cultivated in the Pacific for its esteemed timber. It grows well in the Pacific where it is free of natural pests and is considered a low risk of becoming an invasive naturalized weed. Not many native Meliaceae species occur in Micronesia, though recent molecular studies (Muellner et al. 2005) have indicated that some complex and variable species, following Pannell's wide species concept (1992), contain more than one taxon each. Both *Aglaia palauensis* and *A. ponapensis* were reduced to synonymy under *A. mariannensis* in Pannell's revision (1992). These taxa may be revived pending the results of future molecular work on the Micronesia populations. *Aglaia* is an Indomalayan genus of over 100 arborescent species mostly found in the moist tropics. In Micronesia they occur as small understory trees with new growth that has a conspicuous reddish brown pubescence. The Marianas population is restricted to limestone forest communities, while the Palau and Eastern Caroline populations are found on both volcanic and limestone forests.

Aglaia mariannensis Merr.	Micronesia	G	T(u)	C

MORACEAE
4/11(2)

The fig family has about 1125 species mostly in the tropics and particularly abundant in the lowland rainforests of Africa and the Americas. All species have conspicuous milky white latex, and many species have alternate leaves with a prominent terminal sheathing stipule. *Ficus* is by far the largest genus in the family with 800 species. Micronesia has several native *Ficus* species but only one endemic. *Ficus saffordii*, known from Marianas and Palau, is a large banyan fig that starts out as an epiphyte. It was treated as a variety of *F. microcarpa* by Stone (1970) but is currently recognized as a distinct species (Berg & Corner 2005). *Artocarpus* is a Malesian and Pacific genus with 45 species. Several species are cultivated for food and timber including *A. heterophyllus*, commonly known as jackfruit, and several species of breadfruit including *A. mariannensis*, which was not recognized by Berg et al. (2006) in their Flora Malesiana treatment. They treat it as a synonym of *A. altilis*, which is regarded as an introduction to Micronesia. However, *A. mariannensis* (dugdug or chebiei) is a seeded breadfruit that grows wild in Palau and the

Mariana Islands and has long been cultivated throughout Micronesia, especially on the atoll islands. It hybridizes naturally with the introduced breadfruit *A. altilis,* and the numerous hybrids are only found in Micronesia (Ragone 2010, www.ntbg.org/breadfruit/breadfruit/). Breadfruit is an important staple on Pohnpei particularly and to a lesser extent on other islands in Micronesia. It is also the favored timber for constructing outrigger canoes because of its durability and light-weight.

Artocarpus mariannensis Trecul	Micronesia	L	T	--
Ficus saffordii Merr.	Micronesia	--	E-T	--

MYRTACEAE
3/12(7)

Myrtaceae is a large tropical to warm-temperate family of over 4,600 species. They generally have opposite leaves with gland dots and ethereal oils that make the leaves aromatic when crushed. The bark is often flakey and the stamens are often colored and numerous. *Syzygium*, a palaeotropical genus of over 1,000 species, has often been confused with *Eugenia.* Its center of diversity is in Southeast Asia, where there are many undescribed species. *Eugenia* is now recognized as a neotropical-centered genus, though a few such as *E. reinwardtiana*, native to Australia, Southeast Asia, Micronesia, and other Pacific Islands, do occur outside this range. Fosberg et al. (1979) treated all of the Micronesia plants in this complex under *Eugenia*. Most of these have been transferred back to their previous names under *Syzygium* while others are retained as *Eugenia.* For two, *Syzygium thompsonii* and *Syzygium trukensis,* new combinations were required. We follow Schmid's (1972) treatment for distinguishing *Eugenia* and *Syzygium* in Micronesia and found the material fits this classification scheme. Micronesia's *Eugenia* species were formerly treated as *Jossinia* and many of the *Syzygium* species were formerly treated as *Jambosa*. The two Marrianas endemics in *Eugenia* are very closely allied and were even suspected by Stone (1970) to be potentially different growth forms of the same species. Both names are retained here until molecular or others studies provide evidence to support their synonymy.

Eugenia bryanii Kaneh.	Guam	--	S	--
Eugenia palumbis Merr.	Marianas	L	S	C
Syzygium thompsonii (Merr.) N. Snow	S. Marianas	L	T(c)	--
Syzygium trukensis (Hosok.) Costion & E. Lucas	Chuuk	--	--	--
Myrtella bennigseniana (Volk.) Diels	Micronesia	V	S	--
Syzygium palauensis (Kaneh.) Hosok.	Palau	G	T	--
Syzygium stelechanthum (Diels) Glassman	E. Carolines	V	T-S	--

OLEACEAE
2/2(1)

The olive family contains over 600 species worldwide, all woody. The leaves are opposite, lacking stipules, and may be simple or compound. The flowers are four to five-merous, often aromatic, and are especially distinctive by nearly always having only two stamens. Aside from olives, other economically important members this family include many ornamentals such as lilacs, jasmines, and forsythia. Micronesia's endemic, *Jasminum marianum,* is common and widespread on open limestone forests in the Marianas.

Jasminum marianum DC.	Marianas	G	S	C

PHYLLANTHACEAE
8/25(13)

Phyllanthaceae, a family of 1,745 species worldwide, was split from Euphorbiaceae as a result of molecular studies and various morphological features. Phyllanthaceae species lack latex, the leaves often have petioles with a pulvinus at the base and lack glands, and the fruits have two seeds in each carpel. Many species also have an explosively dehiscent fruit that leaves a persistent central column behind. Both *Cleistanthus* and *Glochidion* are palaeotropic genera with about 140 and 300 species respectively. Wagner & Lorence (2011) recently transferred the Pacific oceanic island *Glochidion* species into *Phyllanthus* and we cite their new names in parentheses below each basionym. This group is very speciose in the Pacific and Micronesia specifically. The expanded genus *Phyllanthus* comprises over 1300 species. Species in the *Glochidion* group can be difficult to differentiate and require further in-depth revision. The Micronesian *Phyllanthus* taxa are distinctive with small and numerous, two-ranked leaves making them very easy to identify in the field. They occur either in the savannahs (*P. palauensis* and *P. saffordii*), or on limestone bluffs (*P. marianus* and *P. rupiinsularis*).

Cleistanthus carolinianus Jabl.	Palau	G	T	U
Cleistanthus insularis Kaneh.	Palau	V	T	U
Cleistanthus morii Kaneh.	Chuuk	--	T	--
Glochidion kanehirae Hosok.	Carolines	--	--	--
(=*Phyllanthus kanehirae* (Hosokawa) W.L. Wagner & Lorence)				
Glochidion macrosepalum Hosok.	Palau	G	S	--
(=*Phyllanthus macrosepalus* (Hosokawa) W.L. Wagner & Lorence)				
Glochidion marianum Muell.-Arg.	Guam	G	T-S	C
(=*Phyllanthus mariannensis* W.L. Wagner & Lorence, nom. nov.)				
Glochidion palauense Hosok.	Palau	G	T	C
(=*Phyllanthus otobedii* W.L. Wagner & Lorence)				
Glochidion ponapense Hosok.	Pohnpei	V	T-S	--
(=*Phyllanthus ponapense* (Hosokawa) W.L. Wagner & Lorence)				
Glochidion senyavinianum Glassman	Pohnpei	V	T-S	--
(=*Phyllanthus senyavinianus* (Glassman) W. L. Wagner & Lorence)				
Glochidion websteri Fosberg	Palau	--	--	--
(*Phyllanthus websteri* (Fosberg) W. L. Wagner & Lorence)				
Phyllanthus marianus Muell.-Arg	Micronesia	L	S	A
Phyllanthus palauensis Hosok.	Palau	V	S	C-A
Phyllanthus rupiinsularis Hosok.	Palau	L	S	--
Phyllanthus saffordii Merr.	Marianas	V	S	--

PUTRANJIVACEAE
1/5(5)

This family was formerly included in Euphorbiaceae, but molecular work has placed it as a separate lineage in its own family. It is a small pantropical family with only three to four genera and 210 species, 200 of which are in *Drypetes.* They have two ranked leaves that are often asymmetrical at the base. The fruits are one-seeded and have persistent flap-like stigmas at the apex. The leaves of many species contain mustard oils and are reported to have a peppery taste. The endemics are found in the Western Carolines and Northern Marianas. *Drypetes dolichocarpa* is only known from Saipan, and *D. rotensis* is only known from Rota.

Drypetes carolinensis Kaneh.	Yap	--	T	--
Drypetes dolichocarpa Kaneh.	Marianas	--	T	--
Drypetes nitida Kaneh.	Palau	G	T	C
Drypetes rotensis Kaneh.	S. Marianas	--	T	--
Drypetes yapensis Tuyama	Yap	--	T	--

PRIMULACEAE
5/14(13)

Recent molecular studies suggest that Myrsinaceae is not a monophyletic family. Myrsinaceae was traditionally separated from Primulaceae on the basis of it members being woody verses herbaceous taxa in the latter. Molecular evidence has shown that many herbaceous taxa from Primulaceae are included within Myrsinaceae. Field characters for distinguishing the woody Primulaceae however are still good. They have characteristic “dash” or line shaped punctations visible when held to light. Some have dot and dash shaped punctations. Only one herbaceous Primulaceae species is present in Micronesia, *Lysimachia mauritiana,* and it has a widespread distribution across the Pacific. All woody species of Primulaceae in Micronesia are endemic. Some, such as *Maesa palauensis* are widespread commonly occurring species, though not locally abundant. Others such as *Maesa canfieldiae* are rare and poorly known. *Discocalyx ladronica* is so poorly known that its island locality within the Marianas is totally unknown. It is only known from the type collection and allegedly very distinct from the more common *D. megacarpa*. Stone (1970) suggested a potential locality mix up; however, it is also certainly feasible that it may have become rare or even possibly extinct after or during WW II. Species of *Myrsine* can often be distinguished by their leaves, which are rather densely clustered near the ends of branches with reddish-purple petioles.

Discocalyx ladronica Mez	Marianas	--	--	--
Discocalyx megacarpa Merr.	Marianas	L	S	C
Discocalyx mezii Hosok.	Palau	G	T(u)	U
Discocalyx palauensis Hosok.	Palau	L	T	--
Discocalyx ponapensis Mez	Pohnpei	V	T-S	--
Embelia palauensis Mez	Carolines	V	WL	--

Maesa canfieldiae Fosberg & Sachet	Palau	L	T-S	RR
Maesa carolinensis Mez	E. Carolines	V	T-S	--
Maesa palauensis Mez	Palau	L	S	--
Maesa walkeri Fosberg & Sachet	S. Marianas	--	T-S	--
Myrsine carolinensis (Mez) Fosberg & Sachet	Pohnpei	V	T-S	--
Myrsine ledermannii (Mez) Fosberg & Sachet	Pohnpei	V	T-S	--
Myrsine palauensis (Mez) Fosberg & Sachet	Palau	V	T(u)	C

RHAMNACEAE

4/4(2)

Rhamnaceae, the buckthorn family, has over 900 species worldwide, mostly trees and shrubs, or sometimes climbers. They are most easily recognized by their flowers having stamens opposite the petals, which are often hood or cup shaped surrounding the stamens. The petals are often smaller than the sepals and can fall off, making it easy to confuse the sepals for petals. Many species are thorny and some are nitrogen fixing. *Alphitonia* is a small genus distributed from Southeast Asia into the Pacific. *Alphitonia carolinensis* is common in the Western Carolines and is most abundant in canopy gaps and edges of savannas. *Ventilago* is also a small genus, palaeotropic in distribution with most species occurring in Australasia. Although *V. nisidai* is not very well known, it has been recorded as a liana collected from the edge of swamp forest on Babeldaob.

Alphitonia carolinensis Hosok.	W. Carolines	V	T	C
Ventilago nisidai Kaneh.	Palau	V	WL-S	--

RUBIACEAE

22/66(45)

Rubiaceae, the coffee family, is the third largest native vascular plant family in Micronesia and the second largest in terms of number of endemic species, exceeded only by the orchids. Members of this family can easily be recognized vegetatively. They have opposite leaves with an inter- or intrapetiolar scar or stipule. The stipule or stipule scar extends across the stem at the node between the two petiole bases. The flowers have an inferior ovary and there is often a scar at the fruit apex left by the calyx and fallen corolla. Micronesia has a number of narrow endemics in this family including *Hedyotis kanehirae,* known only from Alamagan and *Timonius salsedoi*, known only from the island of Malakal. *Hedyotis, Psychotria,* and *Timonius* are by far the most speciose genera in Micronesia. *Hedyotis* is a palaeotropical genus most diverse in SE Asia. Many species in this genus have been transferred back and forth from *Oldenlandia*, which is represented in Micronesia by one native and several weedy species. In Micronesia, *Hedyotis* species range from very small herbs to large shrubs and occur in open savannas, clearings, and under the forest canopy. *Psychotria* is one of the largest of Angiosperm genera with perhaps 1,650 species (Nepokreoff et al. 1999). Most of the Micronesian endemics are shrubs or small understory trees. One of particular interest, *P. diospyrifolia,* occurs as a climber or scandent shrub, which is rare for the genus. *Timonius* is a palaeotropic genus of 150-180 species. These plants are dioecious trees or shrubs with axillary inflorescences.

All of Micronesia's endemics in *Timonius* are restricted to the Western Carolines with the exception of *T. ledermannii* which is endemic to Chuuk and Pohnpei.

Atractocarpus carolinensis (Valeton) Puttock	Carolines	--	T	--
Badusa palauensis Valeton	Palau	G	T	C
Bikkia palauensis Valeton	Palau	L	S	C
Hedyotis aimiriikensis Kaneh.	Palau	V	S	--
Hedyotis cornifolia Kaneh.	Palau	V	H	--
Hedyotis cushingiae Fosberg	Yap	V	D	--
Hedyotis divaricata (Valeton) Hosok	W. Carolines	V	S	--
Hedyotis fruticulosa (Volk.) Merr.	Micronesia	V	S	--
Hedyotis kanehirae (Hatusima) Fosberg	N. Marianas	V	S	RR
Hedyotis korrorensis (Valeton) Hosok	Palau	V	S	C-A
Hedyotis laciniata Kanehira	Marianas	V	H	--
Hedyotis megalantha Merr.	Guam	V	H	--
Hedyotis ponapensis (Valeton) Kaneh.	E. Carolines	V	H	--
Hedyotis sachetiana Fosberg	Palau	V	S	--
Hedyotis scabridifolia Kaneh.	Marianas	V	H-S	--
Hedyotis suborthogona Hosok.	Palau	V	H	--
Hedyotis tomentosa (Valeton) Hosok.	Palau	G	H	C
Hedyotis tuyamae Hosok.	Palau	V	S	--
Hedyotis uncinelloides (Valeton) Hosok.	Pohnpei	V	H	--
Ixora casei Hance	Micronesia	G	S	C
Ixora triantha Volk.	Micronesia	--	S	C
Morinda latibractea Valeton	Palau	L	T(u)	U
Morinda pedunculata Valeton	Palau	V	S-T	C
Ophiorrhiza palauensis Valeton	Palau	G	H	U
Psychotria andersonii Fosberg	Guam	--	--	--
Psychotria arbuscula Volk.	Yap	--	S	--
Psychotria cheathamiana Kaneh.	Palau	L	T(u)	--
Psychotria diospyrifolia Kaneh.	Palau	V	WL-S	U
Psychotria hombroniana (Baill.) Fosberg	Micronesia	G	S	--
Psychotria hosokawae Fosberg	Kosrae	V	T-S	--
Psychotria lasianthoides Valeton	Pohnpei	V	S	--
Psychotria malaspinae Merr.	Guam	--	S-T	--
Psychotria mariana Bartl. ex DC.	Micronesia	L	T	C
Psychotria merrillii Kaneh.	Pohnpei	V	T-S	--
Psychotria mycetoides Valeton	Palau	V	S	--
Psychotria rhombocarpa Kanehira	Kosrae	V	T-S	C
Psychotria rhombocarpoides Hosok.	Pohnpei	V	S	--
Psychotria rotensis Kaneh.	Micronesia	G	T-S	--
Timonius albus Volk.	Yap	--	T-S	--
Timonius corymbosus Valeton	Palau	G	T-S	--
Timonius ledermannii Valeton	E. Carolines	V	T	--
Timonius korrensis Kaneh.	Palau	L	T	--
Timonius mollis Valeton	Palau	V	T(u)	--

Timonius subauritus Valeton	Palau	V	S	C
Timonius salsedoi Fosberg & Sachet	Palau	V	T(u)	RR

RUTACEAE

2/5(3)

Rutaceae is the citrus family with over 1800 species worldwide. The leaves are usually opposite and often compound with distinct gland dots. The foliage of species with simple leaves could potentially be confused with Myrtaceae, which also have opposite leaves with gland dots. The aroma of the oils present in the citrus family however, is noticeably different from Myrtaceae when the leaves are crushed. *Melicope* has 150-233 species distributed from Madagascar and the Indo-Himalaya region east to Hawaii and the Marquesas. There are different viewpoints on the generic limits of this genus, though these do not affect the status of the Micronesian taxa. In Micronesia *Melicope* occurs as a shrub or small understory tree and is more or less inconspicuous. *Melicope ponapensis* has unifoliate leaves that are opposite or in whorls. Both Palau species have trifoliate leaves and are very similar. *Melicope trichantha* occurs on volcanic islands, while *M. palawensis* occurs on limestone islands. *Melicope trichantha* also has stouter branchlets and petioles, and the petals and sepals are larger with a velvety pubescence (Hartley 2001).

Melicope palawensis (Lauterb.) T.G.Hartley	Palau	L	S	C
Melicope ponapensis Lauterb.	Pohnpei	V	T-S	--
Melicope trichantha (Lauterb.) T.G.Hartley	Palau	V	S-T	--

SAPINDACEAE

7/9(3)

Sapindaceae is a large family distributed worldwide. It was recently expanded to include Aceraceae, the maples, and other small groups. They are an important family in tropical Australia and Southeast Asia. Tropical members can usually be distinguished by their pinnately compound leaves with a small terminal rachis tip protruding at the leaf apex, ridged rachis, and swollen petioles. Most Sapindaceae flowers have an extrastaminal disc, a nectary disc that occurs outside the whorl of stamens, or the whorl of stamens sits on top of the disc. This a unique character among the flowering plants, most nectary discs being intrastaminal, occurring inside the whorl of stamens. *Allophylus holophyllus* was noted by Stone (1970) to be rare on Guam and potentially synonymous with *A. timorensis*, though he did distinguish it from the latter by having an entire leave margin and densely pubescent inflorescence axis. We retain the name until molecular data or other studies prove otherwise. *Cupaniopsis guillauminii* has been placed under several different names spanning three genera over the years. Van der Ham (1977) made the correct combination under *Cupaniopsis* but incorrectly included the Fijian endemic *C. concolor*. This species concept was subsequently rejected by both Smith (1985) and Adema (1991), thus both the Chuuk and Fiji endemics are retained. We only know *Elattostachys palauensis* from the type specimen, which was collected from the limestone Rock Islands in Koror State.

Allophylus holophyllus Radlk.	S. Marianas	L	S	R

Cupaniopsis guillauminii (Kaneh.) Adema	Chuuk	--	T	--
Elattostachys palauensis Hosok.	Palau	L	T	--

SAPOTACEAE
3/5(3)

Sapotaceae is a tropical family with roughly 1,100 known species. They have alternate leaves often clustered toward branch tips with white latex. The terminal buds are often covered with brownish appressed hairs and the petioles are often described as bottle shaped. The genus *Manilkara* is currently under revision. Preliminary molecular results suggest that the genus is not monophyletic and the Palau species along with others may be transferred to a different genus. *Manilkara udoido* is a distinctive tree with a curious distribution, only occurring in southern Babeldaob, where it can form dominant stands. The two Micronesian species of *Planchonella*, *P. obovata* and *P. calcarea*, were placed in *Pouteria* by Fosberg et al. (1979), but they have both been transferred back to *Planchonella*. *Planchonella calcarea* is poorly known. It probably occurs throughout the limestone islands of Palau but has only been recorded from one locality aside from the type and was noted to be rare (Fosberg and Sachet 1980). *Palaquium* is a genus of about 120 species from Southeast Asia to Australia and the Pacific. The latex of some species has been intensively studied and exploited for its excellent electrical insulating properties. *Palaquium karrak* is a tall canopy tree occurring in the lowland forests of Pohnpei.

Manilkara udoido Kaneh.	Palau	V	T	A,RR
Palaquium karrak Kaneh.	Pohnpei	V	T	--
Planchonella calcarea (Hosok.) P. Royen	Palau	L	T	--
Planchonella micronesica (Kaneh.) Kaneh. ex H.J. Lam	Kosrae	V	--	--

SALICACEAE
4/6(3)

Many of the tropical members of this family were traditionally placed in a separate family, Flacourtiaceae. This family was never regarded as a solid natural group but has only recently been dissolved and divided into several separate, unrelated families. All of the Micronesian taxa were transferred to Salicaceae except for *Pangium edule*, the football fruit, which was transferred to Achariaceae. Salicaceae have distinct “salicoid” teeth or serrations on the leaf blade, which are unique by having a vein extending to the apex of the tooth, which is tipped by a circular gland or hair. *Casearia* is a tropical genus of roughly 180 species. They are notoriously difficult to distinguish, and a good hand lens or a dissecting microscope is required for the Micronesian taxa. *Xylosma* is a pantropical genus containing about 85 species. They are often small shrubby plants with thorns and many are used for ornamental hedges. The Micronesian endemic, *X. nelsonii*, is an unarmed shrub occurring in open areas along the coast or in savannahs. It is only known from the Marianas and Chuuk.

Casearia cauliflora Volk.	Yap	--	T	--

Casearia hirtella Hosok.	Palau	G	T	C
Xylosma nelsonii Merr.	Micronesia	V	S	--

SOLANACEAE

2/4(2)

Solanaceae is the nightshade family, which is famous for both its many poisonous and nutritious plants. There are some 2,460 species found worldwide. A great number have been exploited by humans, some for the sustenance they provide such as tomato, potato, chili, eggplant, and goji berries, and others for their alkaloids such as tobacco, *Datura*, and *Brugmansia*. *Solanum* is the largest genus with 1,200-1,700 species. The genus occurs worldwide but is most diverse in South America. *Solanum guamense* is endemic to the Marianas and only occurs on limestone cliffs along the coast. *Solanum mariannense* is very poorly known and has only been recorded from the island of Rota (Fosberg et al 1979).

Solanum guamense Merr.	Marianas	L	S	--
Solanum mariannense Hosok.	S. Marianas	--	S	--

URTICACEAE

11/24(7)

The Urticaceae is the stinging nettle family. To “urticate” means to produce a stinging or itching sensation. Many members of this family have glandular hairs that contain mild to severe neurotoxins in them. The sting can vary from a mild itch, as in many temperate herbaceous *Urtica* species, to severe pain requiring medical attention as in some arborous *Dendrocnide* species. *Dendrocnide latifolia*, native to Micronesia can produce a mild but harmless sting. The flowers of this family are small and mostly wind pollinated and thus distinctively non-showy. *Elatostema* is a large genus of some 300 palaeotropic species. The species generally occur as herbs to small shrubs without stinging hairs. Many of the Micronesia endemics occur as herbs along riverbanks where it is moist year round. *Pipturus* is an Australasian genus of approximately 50 species stretching from Madagascar to the Pacific. It has radiated substantially in the Pacific, especially Hawaii. The Palau endemic *Pipturus micronesicus* may be derived either from the widespread strand plant *P. argenteus*, or from *P. subinteger*, both native to Palau. It is very poorly known.

Elatostema calcareum Merr.	Micronesia	L	H	--
Elatostema fenkolense Hosok.	Kosrae	V	H	--
Elatostema flumineorupestre Hosok.	Pohnpei	V	H	--
Elatostema kusaiense Kaneh.	E. Carolines	V	H	--
Elatostema stenophyllum Merr.	Guam	V	H	--
Elatostema stoloniforme Kaneh.	Palau	V	H	--
Pipturus micronesicus Kaneh.	Palau	L	S	--

VITACEAE

2/5(1)

The grape family contains about 850 species and is found worldwide, though it is more abundant in the tropics. The leaves are palmately compound, veined, or lobed. Vitaceae vines and lianas can be distinguished from other vines by the tendrils that occur directly opposite the leaves at a 180° angle. The family is represented by two native genera in Micronesia. *Leea* was formerly placed in its own family, Leeaceae. It is now placed as subfamily Leeoidea within the Vitaceae. *Leea guineensis* and *L. indica* are both widespread species that occur as understory trees or shrubs in the Indomalesian region. *Cayratia* is represented by over 60 species in the palaeotropics and Pacific. Preliminary molecular work indicates it is a paraphyletic genus (Soejima 2006). Of the three native *Cayratia* species in Micronesia, one is allegedly endemic to Palau. It is so poorly known that the only information about the species is from the protologue and type specimen.

Cayratia palauana (Hosok.) Suesseng.	Palau	L	WL	--

NEW COMBINATIONS AND NAMES

THELYPTERIDACEAE

We follow Smith et al. (2006) in their circumscription of Thelypteridaceae genera. The five species listed below are now referable to *Cyclosorus* Link, and therefore require the following new combinations in that genus.

Cyclosorus carolinensis (Hosokawa) Lorence, **comb. nov.**
Basionym: *Dryopteris carolinensis* Hosokawa, Trans. Nat. Hist. Formosa 26: 74. 1936. Type: Palau Is. Todai-san, 15 Oct. 1933, *Hosokawa 7518* (Holotype TAI; Isotype BISH 498211!). *Christella carolinensis* (Hosokawa) Holttum, Kew Bull. 31: 307. *Thelypteris carolinensis* (Hosok.) Fosberg, Smithsonian Contr. Bot. 45: 4. 1980.
Note: The club-shaped yellow-orange glands on lower surface of the pinnae are distinctive.

Cyclosorus gretheri (W. H. Wagner) Lorence, **comb. nov**.
Basionym: *Lastrea gretheri* W. H. Wagner, Pacific Sci. 2: 214, fig. 1. 1948. Type: Mariana Islands. Rota, growing on bare coral-limestone rock in crevice in rather exposed situation on a bank along road at 800 ft. altitude on the north slope of the plateau of Rota, 27 July 1947, *D. F. Grether 4468* (Holotype UC; Isotype BISH 498913!). *Thelypteris gretheri* (W. H. Wagner) B. C. Stone, Micronesica 2: 135. 1967. N. Marianas

Cyclosorus guamensis (Holttum) Lorence, **comb. nov**.
Basionym: *Christella guamensis* Holttum, Allertonia 1: 222. 1977. Type: Mariana Islands. Guam, by small stream, *Grether 4384* (Holotype: BISH! Isotype UC). *Thelypteris guamensis* (Holttum) Fosberg & Sachet, Amer. Fern J. 71(3): 82 (1981). 1981.

Cyclosorus palauensis (Hosokawa) Lorence, **comb. nov.**

Basionym: *Meniscium palauense* Hosokawa, Trans. Nat. Hist. Soc. Formosa 28: 148. 1938. Type: Palau, Babeldaob, in a primary forest on Mt. Grittel near Ngakurao, *Hosokawa 9265*. (Holotype: TAI, digital image seen!). *Thelypteris palauensis* (Hosok.) C. F. Reed, Phytologia 17: 300. 1968.

Cyclosorus rupiinsularis (Fosberg) Lorence, **comb. nov**.
Basionym: *Dryopteris rupicola* Hosokawa, Trans Nat. Hist. Soc. Formosa 26: 73. 1936, non C. Chr. 1917. Type: Caroline Islands. Palau, on elevated coral rock, *Hosokawa 7440* (Holotype TAI; digital image seen!; Isotype BISH). G*laphyropteris rupicola* (Hosokawa) Hosokawa, Trans. Nat. Hist. Soc. Formosa 32: 285. 1942. *Christella rupicola* (Hosokawa) Holttum, Allertonia 1: 217. 1977. *Thelypteris rupi-insularis* Fosberg, Smithsonian Contr. Bot. 45: 5 (1980).
Note: There is already a *Cyclosorus rupicola* Ching & K.H. Shing, Fl. Fugianica 1: 598. 1982, based on a different type, thus precluding the use of this epithet. This necessitates using the next available epithet, namely that of *Thelypteris rupi-insularis* Fosberg.

FABACEAE

The basionym *Dalbergia oligophylla* Hosokawa is invalid. It was described by Hosokawa (1934) after *Dalbergia oligophylla* Baker ex. Hutch & Dalziel was validly published in the Flora of West Tropical Africa (Hutchinson & Dalziel 1928). *Dalbergia oligophylla* is endemic to Cameroon and classified as Endangered (Cheek 2004). We therefore propose the following new name for this species.

Dalbergia hosokawae (Hosokawa) Costion **nom. nov.**
Basionym: *Dalbergia oligophylla* Hosokawa, Trans. Nat. Hist. Soc. Formosa 24: 415. 1934. Type: Palau, Ailai & Aimiliiki-son Islands *Hosokawa 7298* (Holotype TAI; Isotype MICH, digital image seen!).

MYRTACEAE

Two species formerly treated under *Eugenia* by Fosberg et al. (1979) are transferred to *Syzygium*. Type material was studied in collaboration with Myrtaceae expert Eve Lucas and the morphology was found to be consistent with Schmid's (1972) classification of *Eugenia* and *Syzygium*. *Eugenia* is mostly restricted to the New World with a few species extending into the Old World and Pacific while *Syzygium* is restricted to the Old World and Pacific. We reject the recent account of Snow and Veldkamp (2010) that merges *Eugenia thompsonii* and *Eugenia trukensis* under one name, *Syzygium thompsonii* (Merr.) N. Snow. The authors did not manually inspect type material of either species and based the merging of the two endemics on digital photos. Further more, the authors ignored obvious discrepancies in substrate types between the two populations. The Marianas population is well known to be restricted to limestone forests. These habitats occur on raised limestone in the Southern Marianas while the type collections of *S. trukensis* are clearly from volcanic soils on Mt. Witipon, Weno (Moen) Island, Chuuk. If the two populations were synonymous then an explanation for its absence on the volcanic soils of Guam is necessary. In addition the authors do not discuss the unlikely probability of such a strange disjunction in Micronesia; restricted to the Southern Marianas and Chuuk. We thoroughly reviewed the literature for the Micronesian flora and are unaware of any plants with such a disjunction. Until sufficient evidence for Snow and Veldkamp's concept of *S. thompsonii* (2010) is provided, we retain the original species concepts of both taxa.

Syzygium thompsonii (Merrill) N. Snow, Austrobaileya 8(2): 182. 2010.
Basionym: *Eugenia thompsonii* Merrill, Phillipp. J. Sci., C 9: 121. 1914, Type: Mariana Islands, Guam. *Jambosa thompsonii* (Merr.) Diels, Engl. Bot. Jahrb. 56: 533. 1921. Type: Mariana Islands, Guam, *Guam Experiment Station/Thompson 469* (Holotype K!).

Syzygium trukensis (Hosokawa) Costion & E. Lucas **comb. nov.**
Basionym: *Eugenia trukensis* Hosokawa, J. Jap. Bot. xiii. 281. 1937. Type: Chuuk islet Wara, *Hosokawa 8434* (Holotype TAI, digital image seen!; Isotype MICH, digital image seen!) *Jambosa trukensis* (Hosok.) Hosok. J. Jap. Bot. 1940, xvi. 545.

UNVERIFIED NAMES

MENISPERMACEAE

Pachygone ledermannii Diels **Allegedly Endemic to: Carolines**
The author of this species maintained four distinct species for Malesia, which were all lumped into one by Forman (1957). *Pachygone ledermannii* is allegedly closely allied with *P. vieillardii* Diels, which itself was found by Forman (1997) to be complicated by having its type specimen comprised of two separate species from different genera. For these reasons and since the Micronesian material has been excluded in the more recent revisions by Forman, we refrain from assigning endemic status to this species until further studies can be done.

Tinospora homosepala Diels **Allegedly Endemic to: Marianas**
Potentially the same as or a variety of *Tinospora glabra* (Burm. f.) Merrill, which is widespread from Malaysia to Philippines, New Guinea, and New Brittain (Forman 1981). The Micronesian plants differ from latter only in having equal sepals, and Forman (1981) notes a variation in sepal length for a specimen *Tinospora glabra* from the Philippines. Fruits of *T. homosepala* are unknown and are required to resolve its taxonomic placement.

DISCUSSION

Table 3 summarizes the results of this paper with the number of endemic plants per island group. The total land area per island group is provided to give additional perspective on the importance of Micronesia's biodiversity. The Caroline Islands comprise less than half the total land area of the region yet contain 77% of all endemic plants found there. Palau alone makes up only 17% of Micronesia's total land area but contains 37% of all endemic plants in Micronesia. The Caroline Islands and Palau in particular, clearly stand out with an exceptionally high endemism and diversity of plant species. Determining the causes and explanations for the unevenness of biodiversity on oceanic islands has generated much interest since MacArthur and Wilson's (1967) theory of island biogeography, but until now addressing the flora of Micronesia as a whole was problematic. It is hoped that in addition to the practical and local benefits for local knowledge and conservation, this checklist will be utilized as a baseline resource for tackling larger questions on island biogeography in the Pacific region and beyond. Addressing such questions exceeds the aims of the present study however to emphasize the biodiversity value of Micronesia on a global scale we compare our diversity results from Micronesia to that of other insular floras and recognized global biodiversity hotspots.

In Table 4 we compare the endemism and diversity of plants found within the major archipelagos of the Micronesia-Polynesia biodiversity hotspot (Conservation International 2007). Up to date and reliable information on the number of indigenous and endemic vascular plants was compiled for the Marquesas (Wagner and Lorence 2002), Fiji (Watling 2005), Samoa (Whistler 1992; Whistler 2011a), the Societies (Florence 1987), Tonga (Whistler 2011b) and Hawaii (Wagner et al. 1990; Palmer 2003). The most commonly utilized approach in botanical and conservation literature to calculate plant endemism is to divide the total number of endemic species by the total number of native or indigenous species. This however only gives a measure of the relative speciation rates of lineages once established and the relative isolation of the respective islands. Species richness or richness of endemic species is more accurately calibrated to space; thus in this case the richness of native and endemic plant species per archipelago is also calculated by dividing the total number of species by the total land area (km^2). When this approach is utilized the Micronesia bioregion clearly has the highest richness of both native and endemic plants in the entire Micronesia-Polynesia biodiversity hotspot. Although biodiversity data for island groups such as the Cook Islands and the Phoenix Islands were not available for comparison, their floras, mostly comprised of atoll vegetation (Mueller-Dombois and Fosberg 1998) except for the high islands of the Cook archipelago, are unlikely to surpass those listed in Table 4. Hawaii is often touted as having one of the highest rates of endemism in the world, but clearly Micronesia has a richness of plant endemism per square kilometer ten times higher than Hawaii.

Micronesia's exceptionally high richness of endemic plant species is not only a regional pattern. When it is compared to the recognized island biodiversity hotspots of the world (Conservation International 2007) it surpasses them all per unit area (Table 4). Only New Caledonia comes close at 13%. New Caledonia is a continental island with ancient Gondwanan links and is thus expected to have an exceptionally unique biota in comparison to oceanic islands. These data suggest that Micronesia is worthy of being recognized as a distinct biodiversity hotspot. Its richness of plant endemism is distinguishable at both the regional and global scales. The consequence of this fact means that establishment of reserve lands in Micronesia has a substantially high efficiency of maximizing species conserved per square kilometer. It also means that here, possibly more than anywhere else, the vulnerability of extinction is extremely high. The tiny islands of Micronesia may be small geographically; however, their importance to the world in maintaining reserves of unique biodiversity is not small by any means. Efforts to increase funding for collaborative projects and opportunities with developed countries to aid in the establishment of protected areas in Micronesia should be given high priority.

The importance of funding alpha taxonomy in the Pacific and other poorly known tropical regions cannot be emphasized enough. While it is common knowledge that we cannot conserve that which we don't know or understand, taxonomy remains a discipline in decline. Many archipelagos in other parts of the Pacific are in need of revised checklists and biodiversity inventories. A potential solution to the decline in taxonomic expertise and funding is to link up with other large funding schemes which are now available for projects relevant to issues such as climate change, the carbon credit scheme, DNA barcoding, and the Tree of Life project. Opportunities such as these can be seized to simultaneously advance alpha taxonomy where it is needed. As the world continues to specialize, taxonomic specialists must broaden their collaborative capacities to achieve outcomes for multiple concurrent platforms.

Lastly, we would like to reiterate Stone’s wish that publishing this list will stimulate further floristic studies of all kinds in Micronesia. We have alluded throughout the text to ideas of potential ancestors of some of Micronesia’s endemic plants well aware of the fact that focused studies must be done for each taxa and respective lineage to reconstruct their evolutionary history. The era of bioinformatics and DNA research is well underway, which has made the tools for answering questions such as these widely available even for small undergraduate student projects. We hope this list may inspire more small projects such as these in Micronesia. Though the islands may be small, the biota they contain is diverse and complex. Recent molecular work has already demonstrated that several genera represented in Micronesia are polyphyletic or paraphyeltic, and that some genera dispersed to islands once and speciated while other genera may have dispersed more than once. We expect that the dispersal patterns and historical biogeography here will be complex, and that the process of unraveling these evolutionary stories will provide much pleasure and interest to both the professional and casual naturalists interested in the tropical Pacific flora.

Table 3: Number of endemic vascular plant species and total land area per island group

Island Group	Land Area (km²)	Endemic Species	% Endemism (Spp./km²)	Sub-Region
Palau	459	135	29%	Western Carolines
Yap	118	9	8%	
W. Carolines	577	16	- - -	
Subtotal	**577**	**160**	28%	
Chuuk	127	16	13%	Eastern Carolines
Pohnpei	345	47	14%	
Kosrae	110	18	16%	
E. Carolines	582	20	- - -	
Subtotal	**582**	**101**	17%	
Carolines	1159	19	- - -	All Caroline Islands
Subtotal	**1159**	**280**	24%	
Guam	541	11	2%	Marianas
S. Marianas	843	16	3%	
N. Marianas	164	5	3%	
Marianas	1007	22	- - -	
Subtotal	**1007**	**54**	5%	
Gilbert Islands	281	1	0.4%	Far Eastern Micronesia
Marshall Islands	181	0	0%	
Micronesia	2628	29	- - -	All Micronesian Islands
Total	**2628**	**364**	14%	

Table 4: Comparison of plant diversity and endemism within and across island biodiversity hotspots.

Archipelago	Size (km²)	Native species (N)	Richness (N/km²)	Endemic species (E)	Endemism (E/N)	(E) Richness (E ssp./km²)
Micronesia-Polynesia Biodiversity Hotspot						
Micronesia	2,628	1,227	47%	364	30%	14%
Marquesas	1,050	362	34%	162	46%	6%
Society Islands	1,598	896	56%	273	43%	6%
Fiji	18,274	1,594	9%	861	54%	5%
Samoa	3,030	550	18%	165	30%	5%
Hawaii	28,311	1,255	4%	1109	88%	4%
Tonga	748	340	45%	15	4%	2%
Island Biodiversity Hotspots of the World						
Micronesia	2,628	- - -	- - -	363	- - -	14%
New Caledonia	18,972	- - -	- - -	2,478	- - -	13%
Polynesia-Micronesia	47,239	- - -	- - -	3,074	- - -	7%
East Melanesia	99,384	- - -	- - -	3,000	- - -	3%
Caribbean Is.	230,000	- - -	- - -	6,550	- - -	3%
Philippines	297,179	- - -	- - -	6,091	- - -	2%
Madagascar	600,461	- - -	- - -	11,600	- - -	2%
New Zealand	270,197	- - -	- - -	1,865	- - -	0.7%
Japan	373,490	- - -	- - -	1,950	- - -	0.5%
Wallacea	338,494	- - -	- - -	1,500	- - -	0.4%

ACKNOWLEDGEMENTS

This work was supported by an Australian Postgraduate Fees Scholarship from the University of Adelaide and the Australian Tropical Herbarium. We would like to thank the following people for supporting the project and or providing helpful information on taxonomy of particular species or help with determining specimens: Darren Crayn, Andrew Lowe, Ed Biffin, Eve Lucas, and Allen R. Smith. We would also like to acknowledge all the people that contributed to progress of this work by collaborating on checklists for subregions within Micronesia: Ann Kitalong, Mike Balick, Tarita Holm, Robin DeMeo, Tim Flynn, and Art Whistler. We also thank the curators of the Bernice P. Bishop Museum (BISH) and National Tropical Botanical Garden (PTBG) herbaria for access to specimens and data.

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CHAPTER 4

Plant DNA barcodes can accurately estimate species richness in poorly known floras.

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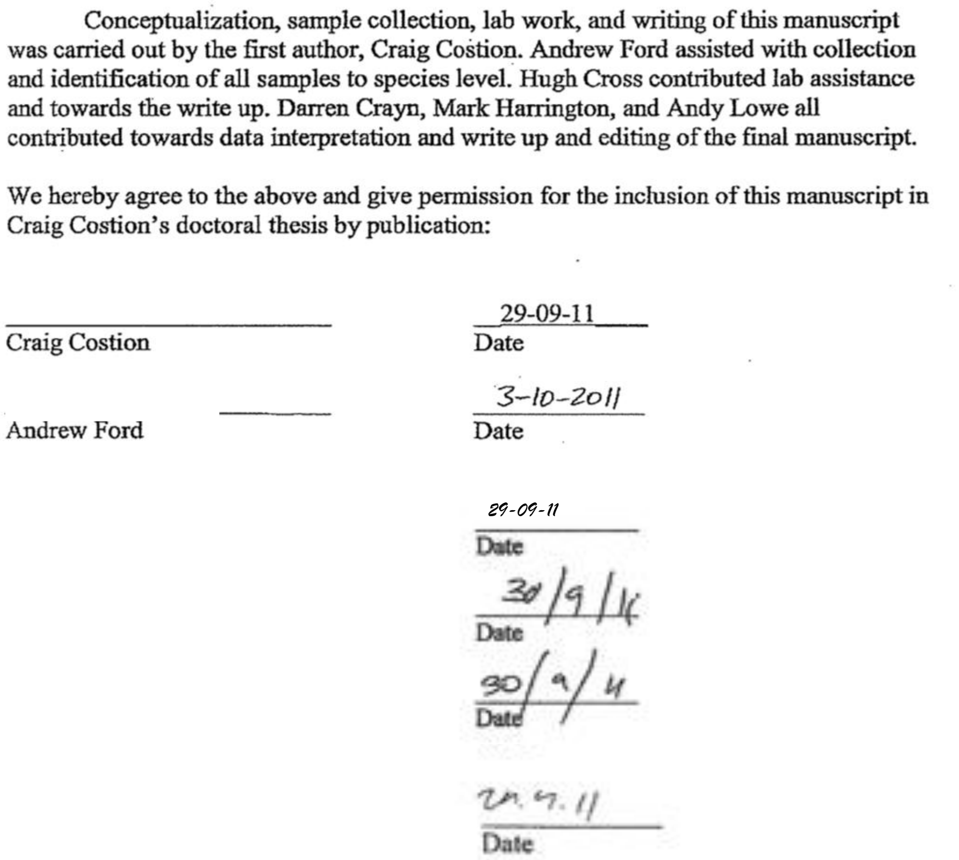
PLoS ONE 6(11): e26841. doi:10.1371/journal.pone.0026841, 2011

Declaration of authorship



Conceptualization, sample collection, lab work, and writing of this manuscript was carried out by the first author, Craig Costion. Andrew Ford assisted with collection and identification of all samples to species level. Hugh Cross contributed lab assistance and towards the write up. Darren Crayn, Mark Harrington, and Andy Lowe all contributed towards data interpretation and write up and editing of the final manuscript.

We hereby agree to the above and give permission for the inclusion of this manuscript in Craig Costion's doctoral thesis by publication:

Craig Costion — 29-09-11 Date

Andrew Ford — 3-10-2011 Date

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ABSTRACT

Background. Widespread uptake of DNA barcoding technology for vascular plants has been slow due to the relatively poor resolution of species discrimination (~70%) and low sequencing and amplification success of one the two official barcoding loci, *matK*. Studies to date have mostly focused on finding a solution to these intrinsic limitations of the markers, rather than posing questions that can maximize the utility of DNA barcodes for plants with the current technology.

Methodology/Principal Findings. Here we test the ability of plant DNA barcodes using the two official barcoding loci, *rbcL*a and *matK*, plus an alternative barcoding locus, *trnH-psbA*, to estimate the species diversity of trees in a tropical rainforest plot. Species discrimination accuracy was similar to findings from previous studies but species richness estimation accuracy proved higher, up to 89%. All combinations which included the *trnH-psbA* locus performed better at both species discrimination and richness estimation than *matK*, which showed little enhanced species discriminatory power when concatenated with *rbcL*a. The utility of the *trnH-psbA* locus is limited however, by the occurrence of intraspecific variation observed in some angiosperm families to occur as an inversion that obscures the monophyly of species.

Conclusions/Significance. We demonstrate for the first time, using a case study, the potential of plant DNA barcodes for the rapid estimation of species richness in taxonomically poorly known areas or cryptic populations revealing a powerful new tool for rapid biodiversity assessment. The combination of the *rbcL*a and *trnH-psbA* loci performed better for this purpose than any two-locus combination that included *matK*. We show that although DNA barcodes fail to discriminate all species of plants, new perspectives and methods on biodiversity value and quantification may overshadow some of these shortcomings by applying barcode data in new ways.

INTRODUCTION

Much of the world's plant diversity is concentrated in recognized biodiversity hotspots [1] containing a high percentage of endemic plant species under threat of extinction. Since these hyper-diverse floras are vulnerable to the increasing threats from human activities, methods that enable rapid identification and quantification of species are needed to aid conservation efforts [2, 3]. Traditional methods of biodiversity inventory are time consuming and are dependent on the availability of taxonomic expertise, which is a resource in decline. Identification of plants in tropical rainforests in most cases remains a challenge even for experts [2]. DNA barcoding has the potential to provide an alternative means of estimating species richness without high-level expertise in field identification skills and in a much shorter time frame.

Although the topic of DNA barcoding initially stimulated much debate among scientists, it is now an accepted taxonomic tool with more new and interesting applications of the technology regularly being devised. DNA barcodes are now being utilized and promoted for a variety of biological applications, including; the identification of cryptic species [4, 5], fragments of species such as tree roots [6, 7], detection of invasive species in ecosystems [8, 9], species discovery [10], taxonomic revision [11], unraveling of food webs and predator prey relationships [12], quarantine [13], and the fight against illegal trade of endangered species [14] and illegally logged timber [15]. The use of barcoding technology for biodiversity inventory of plants has been addressed [16], however, to our knowledge only a few studies [2] have simulated an actual field survey that samples all individual plants in a plot or transect and assessed the usability of the approach for non-experts. We are also unaware of any study that has evaluated the effectiveness of the DNA barcoding approach for estimating plant species richness in a taxonomically poorly known flora.

DNA barcoding is often promoted for its ability to increase accessibility of scientific data and new technologies to the general public and non-experts [17] such as biodiversity inventory and field identification of species. Accurate identification of species in poorly known areas using traditional methods can take many years due to lack of knowledge of the flora and/or a lack of seasonal flower and fruit characters that are required for identification. Even when it is present, collecting fertile material is often challenging, as it can be high in the canopy for many species. Conversely, collection of leaf or cambium tissue for DNA extraction requires little effort [18].

In this study we test the utility of plant DNA barcodes to estimate the species richness of a tropical forest on a local scale and to accurately identify the species within it. We simulated a rapid biodiversity inventory in a well-known and studied flora, the Wet Tropics of Northeast Queensland, utilizing the two official barcoding loci [19] and an alternative barcoding locus *trnH-psbA*, by sampling only leaf and cambium tissue that could be obtained easily without collecting from the canopy. Our primary aim was to assess whether a DNA barcoding approach can produce a rapid and accurate estimate of species richness for a locality in which the species are unknown or include cryptic species and/or life stages such as seedlings or tree roots.

DNA barcoding studies to date have primarily focused on asking ‘can barcode data identify these species’. This requires a reference set of sequences representing taxonomically well-defined entities. For many areas of the world this is not possible because the alpha diversity is not adequately documented. We ask the question ‘in the absence of a robust taxonomy can barcode data identify how many species level groups are present and their membership’. This is a novel application of barcode data, which provides a simple, effective and robust means to determine species richness and to sort individuals into hypothetical species as the first critical step for thorough taxonomy.

METHODS

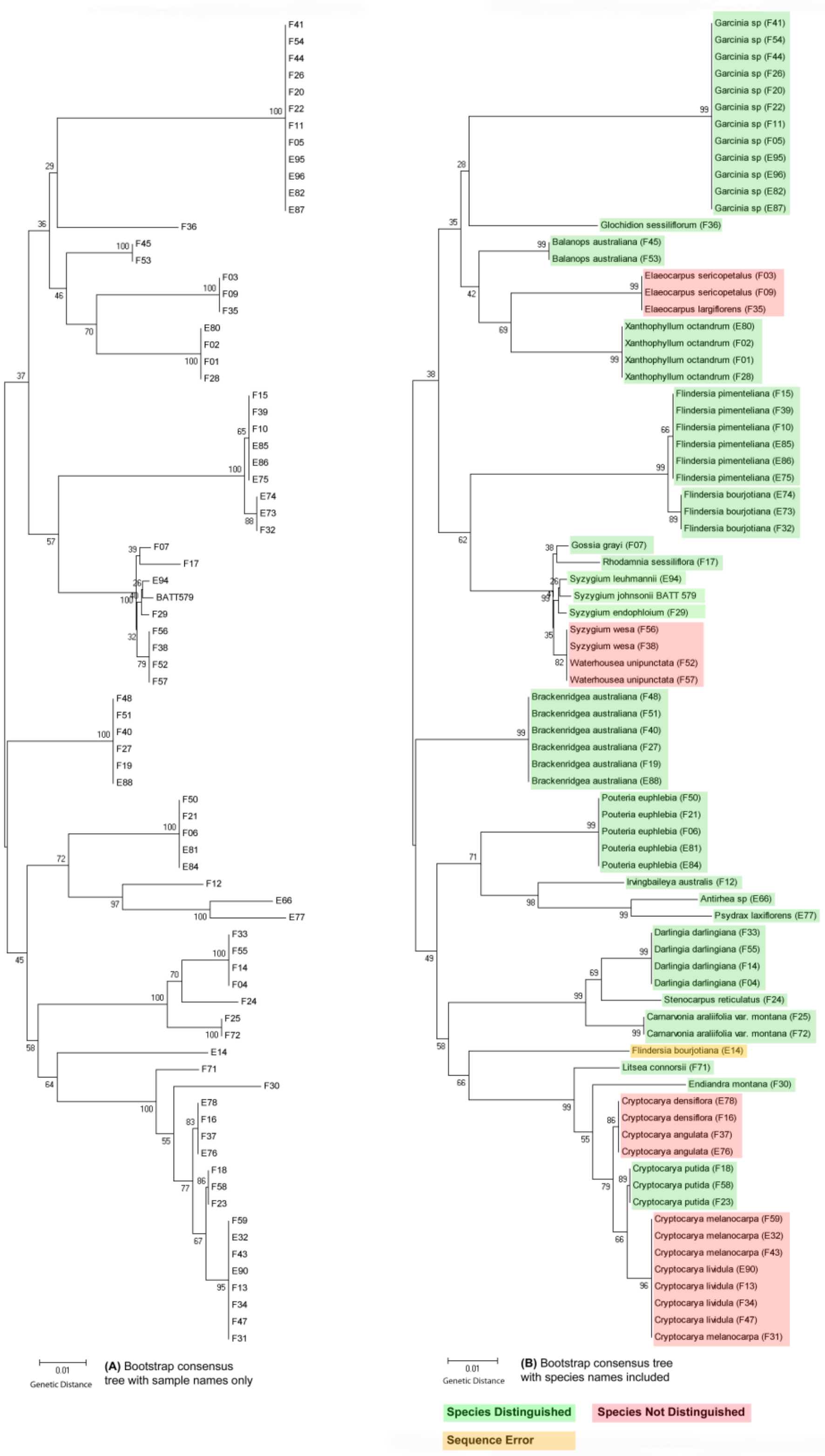
We selected two 0.1 hectare plots as our study sites in tropical northeast Queensland, Charmillan (Plot 1) and Koolmoon (Plot 2), from an existing plot network established by the CSIRO Tropical Forest Research Centre. The two plots occur on the Atherton Tablelands south of Ravenshoe at 720 and 800 meters elevation in simple microphyll and simple notophyll vine forest on rhyolite derived soils. All stems >10 cm dbh were identified and sampled for leaf tissue and/or vascular cambium [18]. Tissue samples were desiccated and preserved in silica gel and voucher specimens (Table S1) were deposited in the local herbarium (CNS). In total, 200 accessions were made representing 58 species spanning 13 orders and 21 families of flowering plants.

Total genomic DNA was extracted from silica-dried samples using the Machery Nagel Plant II DNA Extraction Kit with the PL2/PL3 buffer at the Australian Genome Research Facility (AGRF, Adelaide Australia). Successful amplification of the primary barcoding loci *rbcLa* and *matK* as well as a trial on the alternative barcoding locus *tnrH-psbA* was attempted once for each sample and for a subset of the samples for *trnH-psbA* following the PCR protocol and procedures recommended by the CBOL Plant Working Group [19]. Portions of the three chloroplast loci were amplified using the primers and protocols specified by the plant DNA barcoding working group for the specific regions: for *rbcL*a (550 bp): rbcLa (ATGTCACCACAAACAGAGACTAAAGC) and *rbcL*a (GTAAAATCAAGTCCACCRCG); for the *mat*K region (850 bp): 3F KIM (CGTACAGTACTTTTGTGTTTACGAG) and 1R KIM (ACCCAGTCCATCTGGAAATCTTGGTTC); and *trnH-psbA* (lengths variable): trnHf 05 (CGCGCATGGTGGATTCACAATCC) and psbA3 f (GTTATGCATGAACGTAATGCTC). Thermal cycling parameters for *rbc*L*a* were two minutes at 95°C, 35 cycles of 30 seconds at 95°C, 30 seconds at 55°C, and one minute at 72°C, then final extension for two minutes at 72°C. Cycling conditions for *matK* were five minutes at 94°C, 35 cycles of 30 seconds at 94°C, 20 seconds at 52°C, and 50 seconds at 72°C, then 5 minutes at 72°C. Cycling conditions for *trnH-psbA* were 98°C for 45 seconds, 35 cycles of 98° C for 10 seconds, 64° C for 30 seconds, and 72° for 40 seconds, then 72° C for 10 minutes. PCR products were vacuum dried then purified and sequenced at the Australian Genome Research Facility (AGRF).

Consensus sequences were assembled using ChromasPro v.1.32 and aligned with MAFFT online v. 6, then checked manually with BioEdit Sequence Alignment Editor v.7.0.9.0 [20] (See Tables S2-S3 for complete list of sequences). The final concatenated alignments using the primary barcoding loci *rbcL* and *matK* for each plot (1,479 and 1,474 base pairs) were analyzed separately for genetic distance using neighbor joining trees. Phylogenetic analyses were conducted with MEGA version 5 [21] using the maximum composite likelihood model with 1000 bootstrap replications. Evolutionary distance was measured as the number of base substitutions per site. All positions containing gaps and missing data were eliminated from the analysis. Coding of indels found for some families in the *trnH-psbA* dataset were required to enable species discrimination. Species were distinguished on the basis of observed genetic distance and monophyly of related samples. Monophyletic groups showing zero average pairwise genetic distance between them were treated as distinguished species (Fig. A). Non-monophyletic groups of samples and samples with non-zero average pairwise genetic distance between members of the same species were treated as not distinguished. Species discrimination accuracy was calculated by dividing the total number of species distinguished by the total number of species in the alignment. The total number of species estimated for each plot was calculated from the sum of all monophyletic sample groups in the alignment without any observed genetic distance. Species richness accuracy was then calculated by subtracting the number of amplification errors from the total number of species estimated from the alignment then dividing that figure by the total number of species present in the plot. Amplification errors could be easily identified after trace file inspection (Figure 1) since the species were known and were necessary to account for since they can incorrectly estimate additional species present at the study site and must be accounted for in studies where the identity of samples is unknown.

A trial was run on the alternative barcoding locus *trnH-psbA* by constructing an additional series of alignments on a subset of our samples, to compare its distinguishing power with *matK* and *rbcLa*. Although *trnH-psbA* is not considered an official barcoding locus [19], it is known for its higher sequence recovery rate [22] than *matK*, primarily due to the lack of universality of primers for the latter locus [23]. We generated *trnH-psbA* sequences from all species-rich lineages present in the two plots to compare with the discrimination scores from the *rbcLa* and *matK* data. Lineages represented by only one species were not analyzed with the third marker as there was no question as to the ability of these taxa to be distinguished with only two markers. We also included some additional individuals of the same species collected from localities distant from the two study sites to test for infraspecific variation.

Figure 1: Plot 1 *rbcLa* NJ tree with bootstrap values, displayed without (A) and with (B) species names.*



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* *Pouteria euphlebia = Planchonella euphlebia; Waterhousea unipunctata = Syzygium unipunctatum*

RESULTS

The results of Plot 1 (Charmillan) for the *rbcLa* locus are shown in Figure 1. The same tree is displayed without (Fig. 1A) and with (Fig. 1B) the known species identifications to illustrate the potential of applying this method on cryptic samples and/or an unknown flora. Similar trees were generated for both plots using all loci and locus combinations (Figures S1-S4), and results are summarized in Table 1.

The successful sequence recovery rate for *matK* was substantially lower than for *rbcL*. In most of these cases, PCR amplification was successful for the *matK* sample, but sequence quality was poor. These samples were classified as fails (Table 2). Table 3 shows evidence of species-specific and lineage specific amplification problems for *matK*, particularly in the genera *Garcinia* (Clusiaceae), *Brackenridgea* (Ochnaceae), *Myrsine* (Myrsinaceae), *Elaeocarpus* (Elaeocarpaceae) and the family Rutaceae.

Up to 30% of the sequences obtained with the *rbcLa* marker were unavailable for concatenation due to the poor sequence recovery rate of *matK*. Concatenated data utilized for analysis only included samples, which yielded sequences for both markers. Including samples in the concatenated alignment with only one marker skewed the results substantially for resolving monophyly of species since there was high species redundancy (i.e. many individual plants of the same species) in our sample sites (See Table S2 for complete list of results for each species). Results from *matK* also showed substantially lower species discrimination and richness estimation values (Table 2). Concatenation of both the *rbcLa* and *matK* genes resulted in an identical species discrimination value and lower richness estimation value as inferred from *rbcLa* data alone. Only one species, *Cryptocarya densiflora*, shows any enhanced discriminatory power by the addition of the *matK* gene to *rbcLa*.

Results from the third marker, *trnH-psbA*, showed some increase in discriminatory power at the level of individual species. However, a total of eleven species could not be distinguished with the addition of the third marker. Results for *rbcLa* and *matK* excluding lineages represented by only one species were recalculated (Table 4) for comparison with the alternative barcoding locus *trnH-psbA* A similar pattern to the results from Table 2 is found for *rbcLa* and *matK*. All combinations of *trnH-psbA* have similar performance values and all perform with higher accuracy than the former two loci.

Table 1: Species discrimination and richness estimation accuracy

Locus	Species Resolved	Not Resolved	Estimated from data	Present in alignment	Present in plot	Discrimination accuracy	Estimation accuracy
rbcL	22, 29	8, 12	27, 35	30, 41	31, 42	73%, 71%	84%, 79%
matK	15, 21	11, 14	21, 29	26, 35	31, 42	58%, 58%	58%, 55%
rbcL + *matK*	19, 25	7, 11	25, 35	26, 35	31, 42	73%, 71%	74%, 71%

Units are in species and presented in order by plot number (Plot 1, Plot 2).

Table 2: Sequencing success

Locus	Species Resolved	Not Resolved	Estimated from data	Present in alignment	Present in plot	Discrimination accuracy	Estimation accuracy
rbcL	22, 29	8, 12	27, 35	30, 41	31, 42	73%, 71%	84%, 79%
matK	15, 21	11, 14	21, 29	26, 35	31, 42	58%, 58%	58%, 55%
rbcL + *matK*	19, 25	7, 11	25, 35	26, 35	31, 42	73%, 71%	74%, 71%

Units are in species and presented in order by plot number (Plot 1, Plot 2).

Table 3: Summary of results listed by family

				rbcLa		***matK***		***rbcLa* + *matK***	***trnH-psbA***	***trnH-psbA* + *rbcLa***	***trnH-psbA* + *matK* + *rbcL*a**
Family	**Plot**	**No. Trees**	**G(sp)**	Seq F/E	Spp. D	Seq F/E	Spp. D	Spp. D	Spp. D	Spp. D	Spp. D
ARALIACEAE	K	2	1(1)	0	1	0	1	1	---	---	---
BALANOPACEAE	C, K	5	1(1)	3	1	1	---	---	---	---	---
BURSERACEAE	K	2	1(1)	0	1	0	1	1	---	---	---
CLUSIACEAE	C	12	1(1)	0	1	10	0	0	---	---	---
CUNONIACEAE	K	4	1(1)	0	1	1	1	1	1	1	1
ELAEOCARPACAE	C	8	1(4)	4	1	5	0	0	3	3	3
ESCALLONIACEAE	K	1	1	0	1	0	1	1	---	---	---
ICACINACEAE	C	1	1	0	1	1	1	1	---	---	---
LAURACEAE	C, K	50	3(11)	1	5	4	3	7	5	6	6
MALVACEAE	K	11	1	0	1	0	1	1	---	---	---
MYRSINACEAE	K	6	2	0	1	All	---	---	---	---	---
MYRTACEAE	C, K	17	3(10)	1	6	4	7	7	4	4	6
OCHNACEAE	C, K	7	1	0	1	6	1	1	---	---	---
PHYLLANTHACEAE	C	1	1	0	1	1	---	---	---	---	---

POLYGALACEAE	C	1	1	0	1	0	1	1	---	---	---
PROTEACEAE	K	24	7(7)	0	7	4	5	5	5	5	5
RUBIACEAE	C	3	3(3)	0	3	0	3	3	3	3	3
RUTACEAE	C, K	33	2(4)	4	3	23	2	2	3	2	2
SAPINDACEAE	K	6	3(5)	0	3/2	1	2	2	0	3	3
SAPOTACEAE	C	6	1	1	1	1	1	1	---	---	---
SYMPLOCACEAE	K	1	1	0	1	0	1	1	---	---	---

C = Charmillan, K = Koolmoon, G(sp) = No. of Genera(Species), Seq F/E = Sequence fails and errors, Spp. D = species distinguished, (---) = samples not available to test for indicated marker. Note: Samples of all species not available for *trnH-psbA*

Table 4: Accuracy of loci within speciose lineages represented in plots

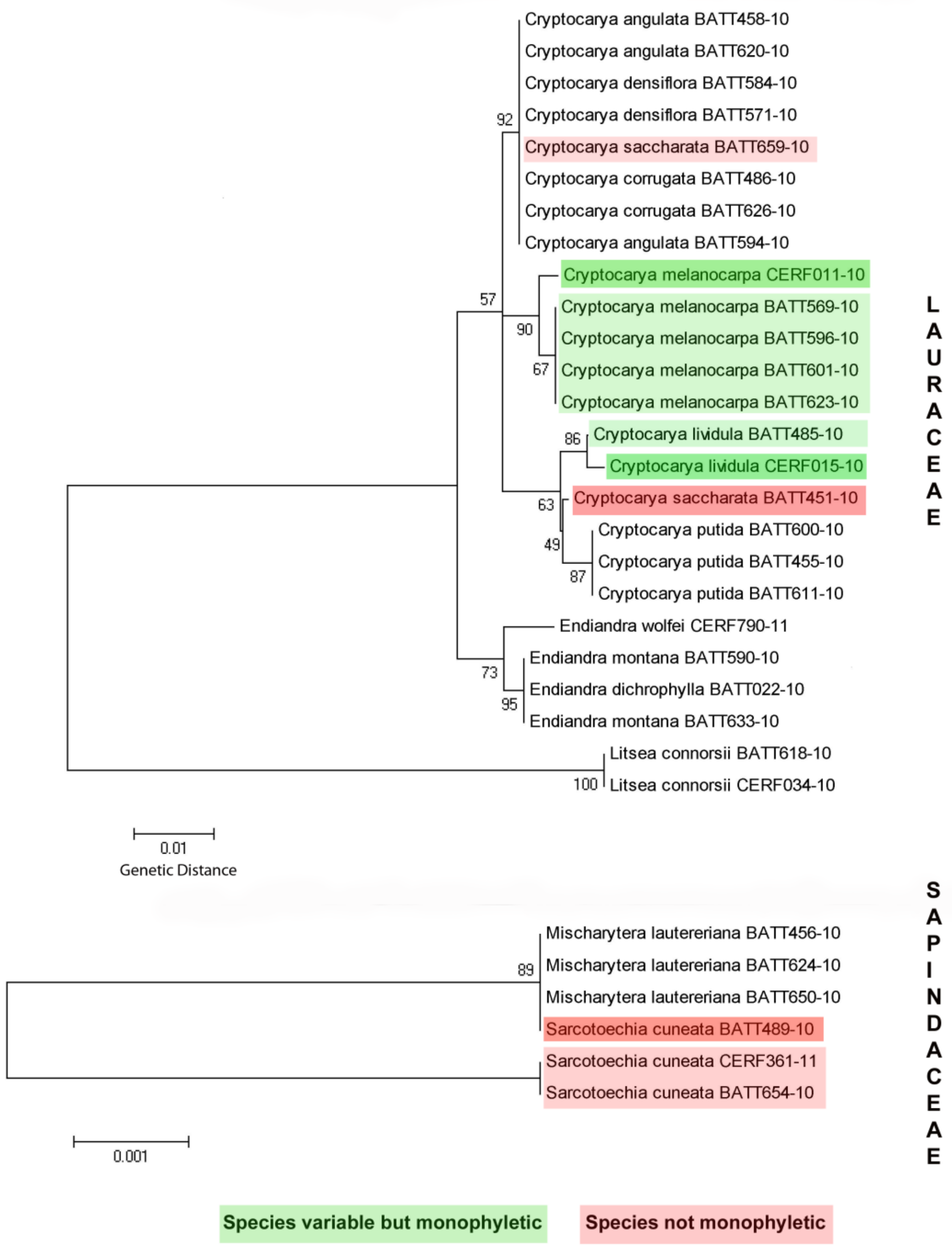
Locus	Species Resolved	Not Resolved	Estimated from data	Present in alignment	Discrimination accuracy	Estimation accuracy
*rbcL*a	25	19	36	44	57%	77%
matK	14	25	27	39	36%	62%
*rbcL*a + *matK*	23	17	37	40	56%	80%
trnH-psbA	23	10	27	33	70%	82%
trnH-psbA + *rbcLa*	26	11	31	37	70%	84%
trnH-psbA + *matK* + *rbcL*a	28	12	33	40	70%	83%

Intraspecific variation due to geographic distance was found in the *trnH-psbA* locus for three species of Lauraceae and one species of Sapindaceae (Figure 2) and obscured the monophyly of two species that would have otherwise been resolved. The intraspecific variation for one species *C. saccharata* BATT451-10 occurs in the form of an inversion of six base pairs, TTTTAT/ATAAAA, which is observed in the same region of the *trnH-psbA* locus that was shown to also have the same effect of confounding species boundaries in Gentianaceae [24].

The accuracy of richness estimation was generally higher than of species discrimination due to the tendency of having two closely related species to be estimated as one. A subset of taxa for example, with four taxa, in which two closely related species are not distinguished, would receive a species discrimination accuracy of 50% (2 unresolved ÷ 4 total present) but an estimation accuracy of 75% (3 estimated ÷ 4 total present).

Low estimation accuracy results are observed for the *matK* locus and the *rbcL* + *matK* combination. This was a direct consequence of lower sequence recovery rate and higher frequency of error from the *matK* dataset. These effects are smoothed out when comparing a more equal subset of taxa across all markers (Table 4) and the *rbcL* + *matK* combination performs slightly higher than *rbcL* alone. All combinations of the *trnH-psbA* locus have higher accuracy of species estimation. The results in Table 4 are actually conservative considering *trnH-psbA* data was only generated for genera with multiple species for comparison to the other loci. This result, when corrected by adding the additional taxa that were represented by only one or two species per family, becomes 88% accuracy of estimation for *trnH-psbA*, 89% for *trnH-psbA* + *rbcLa*, and 88% for *trnH-psbA* + *rbcLa* + *matK*.

Figure 2: NJ tree with bootstrap values showing intraspecific variation in *trnH-psbA*.



DISCUSSION

The results from this study showed that not all species (~30%) could be distinguished, even with a three locus barcode, supporting the findings from much larger datasets that [2, 25] that discrimination of species in the plant kingdom with barcoding loci is inherently challenged by virtue of the evolutionary history of chloroplast genes. Although the number of plots and samples surveyed in this study are relatively low they contain a diverse assemblage of lineages with several species-rich genera and accurately represent the type of diversity that would be expected from a plot sampled from other, more poorly known tropical flora. Fazekas et al. [25] also suggest that using additional markers will not necessarily increase species discrimination power. Our data also support this view, with members of three separate families, Lauraceae, Myrtaceae, and Sapindaceae, containing genera with species that cannot be distinguished with one, two, or three locus combinations (Table S2). Although other authors [16, 26] report higher discrimination rates > 90% from neotropical datasets, we were unable to replicate this level of accuracy even with good sequence data from all three markers. We note that the tendency in the literature is for authors to interpret results such as these as evidence for the inherent faults of DNA barcoding, however, it is well known that there are few people that have the ability to correctly and efficiently identify in a single survey more than 70% of species present in a tropical rainforest plot. An often-posed question in the literature echoes: *to barcode or not to barcode*? We respond: *that is not the question*! It is unreasonable to expect that an emerging method or technology should perform perfectly from the start. DNA barcoding is not an all or nothing endeavor. As the barcoding initiative gains momentum valuable research time is better spent assessing the best applications of the data being generated.

We suggest a new possible application of such data and show that without any taxonomic expertise, a DNA-barcoding approach to floristic inventory can correctly estimate from a single survey the number of species present with almost 90% accuracy. By posing a different question we emphasize through our comparison of species discrimination versus species estimation accuracy the inherent potential of DNA barcoding for plants. This result, albeit tested on a limited dataset of only 200 samples, may prove useful in areas where little taxonomic expertise or local knowledge exists, where repeat surveys to obtain reproductive material often essential for identification are not possible, and/or where conservation priorities need to be made. Although much of the tropics contains a high number of unknown and undescribed plant species, the general floristic composition of most bioregions is well known. A DNA sample-based survey, as simulated in the present study, can be conducted in such a region. Use of existing checklists for the flora of tropical regions could be used to help infer potential species-rich genera that may occur in the survey area. This baseline of knowledge can then be utilized to more accurately calibrate the DNA-based estimate of species richness.

It can be further argued that distinguishing closely related species may not be essential from a biodiversity conservation perspective. Calculating phylogenetic diversity (PD) [27] is now a well-accepted method of measuring biodiversity and assessing conservation priorities [28-30]. The fundamental argument behind PD is that maximizing feature diversity or evolutionary history is more important than maximizing the number of species in a protected area network or reserve. A locality rich in species diversity but represented primarily by one or two species-rich genera that have recently diverged may have less PD and therefore lower biodiversity value than an area with lower or equal species diversity which is composed of more distantly related lineages. Our proposed method of biodiversity survey may have failed to distinguish up to 30% of the species in the present study, however it did capture a nearly complete estimate of the PD present from the sampled sites. A PD value (0.788) was easily calculated for 98% of the species diversity represented in the two plots since only one species failed for all loci. The *rbcL* locus has been utilized as an effective estimate of PD in hyper-diverse floras [29] and is the obvious choice when sampling across all angiosperm lineages. As PD and other PD-related indices continue to gain popularity and acceptance, accurate and rapid methods of estimating PD from poorly known areas to assess their biodiversity value will be required.

In our assessment of loci choice for such rapid biodiversity inventories the *matK* locus in general returned poor levels of success and accuracy while the combination of *rbcLa* and *trnH-psbA* yielded the best results in terms of sequence recovery, time and money invested, and accuracy of both species discrimination and estimation. Their universality in ability to amplify DNA from a diverse subset of angiosperm lineages makes them the most suitable markers for biodiversity surveys. The use of *trnH-psbA* in biodiversity surveys however must be applied with caution due to the intraspecific variation that can occur in this locus.

Intraspecific variation in the *trnH-psbA* locus has been noted in several angiosperm families [24, 31, 32] and Layahe et al. [16] indicated that *trnH-psbA* had the highest intraspecific variation out of all loci tested on a very large dataset. Our results provide additional evidence from two families, Lauraceae and Sapindaceae, for intraspecific variation at the *trnH-psbA* locus that accounts for non-monophyly of species (Figure 2). Further studies are required to test the intraspecific variation of this locus across numerous plant lineages spanning a larger geographical range and larger sampling size. Other problems with the *trnH-psbA* barcode such as length variation, difficulty in alignment [22], and high frequency of mononucleotide repeats that prevent successful bi-directional reads have been discussed and are largely attributed to the lack of consensus for designating it as an official barcode for plants [19]. Our results however suggest that despite these shortcomings, until substantial progress is made with obtaining universal primers for *matK*, the *trnH-psbA* locus performs with much higher accuracy and may be preferred for the purposes of localized biodiversity inventory.

Technical concerns for when the identity of samples is unknown

Some technical concerns require further discussion specifically for the application of a DNA-barcoding based inventory in areas where the samples are unknown to species level or are in a cryptic life stage given the current technology available.

Sample contamination: Samples can be contaminated at various stages in the lab potentially posing a hidden problem. The present study was able to account for all errors because all the species were known and vouchered. In studies where the identity of the samples is not known, this problem can be accounted for by the use of a minimum of two loci, which will enable verification by a GenBank BLAST (Basic Local Alignment Search Tool) search. Alternatively two or three replicates of each sample could be sequenced to assure accurate replication of results.

Trace file interpretation: Even if all lab work is outsourced, interpretation of trace file data is required by an experienced researcher or technician. Ambiguous sites, if not correctly interpreted can incorrectly estimate additional species or diversity within species. Automated trace file editing programs are available but all still require manual checking. This includes sequence data returned from the online barcoding platform Barcode of Life Data System (BOLD) [33], which uses an automated trace file editing program.

Mutliple locus datasets: If the species are unknown, only samples with successful sequences from all utilized loci can be used to avoid over-estimation of species richness. Problems with the universality of the official barcoding locus *matK* specifically present a substantial challenge. Lineage specific *matK* primers have recently been proposed [23], but these still require testing on large-scale datasets from multiple locations around the world before they can be widely adopted.

Coding of gaps: Several informative indels were observed in our alignments of *trnH-psbA,* notably, in Elaeocarpaceae, Sapindaceae, and Rubiaceae. Correct interpretation and coding of such gaps may be required to distinguish species in such lineages. Kress and Erickson [22] suggest that coding of gaps is unnecessary for barcoding since identification will rely primarily on the use of BLAST however reliance on BLAST limits the utility of barcode data to well known and sampled floras and restricts their use on unknown samples or poorly known floras.

CONCLUSION

We conclude by concurring with the response of Kress & Erickson [17] to the fear of some researchers that DNA barcoding will replace the need for taxonomic specialists or divert funds from basic taxonomic research. This has not been proven and in our experience it has provided more funds and staff to address taxonomic research projects with a DNA barcoding component. Recent studies have shown DNA barcodes to be an aid to taxonomic revision or have helped identify cryptic species of plants [34, 35]. Our case of variation within *Cryptocarya melanocarpa* is unlikely a new species but illustrates the utility of DNA barcodes for verifying the assumed identity of plants in living collections and even from voucher specimens identified by experts as shown by Newmaster and Ragupathy [34] for *Acacia,* a notoriously difficult group to identify to species. Lauraceae and many other groups of land plants fall into this category of plants whose identity remains elusive even to experts. DNA barcoding is simply a new emerging tool to aid in this process and more studies and research and development are required for it to reach its maximum potential.

Although follow up studies are required on larger sampling sizes to provide additional support for the findings of the present study, we propose that the barcoding community should focus more effort on new ways to utilize and apply the data being generated. While much of the academic community is still searching for "the holy grail" [36] of plant DNA barcoding, the public and commercial sectors for the most part remain an untapped resource and opportunity. Traditionally access to a fully equipped molecular genetic laboratory facility was mandatory for any DNA sequence based research however today rapid improvements in technology and the costs of outsourcing the work are making DNA-barcoding technology accessible to a larger population of users.

It is also worthy to consider whether DNA barcoding will be advanced by new emerging genomic technologies or become superseded by them. The rapidly advancing field of whole genome sequencing is case in point. It is evident that a silver bullet for plant DNA barcodes remains elusive in the quest to distinguish species with a standardized approach. This clearly reflects the infancy of the emerging science and technology but may also reflect current viewpoints on how we fundamentally value biodiversity (i.e. number of, versus, distinctiveness of taxa) and understand species boundaries. DNA barcoding as we know it today may only be a stepping stone towards a much greater base of both taxonomic knowledge and technological capacity. Creating more links between the academic, public, and commercial sectors in regards to outputs and benefits of the technology, as is being done with whole genome sequencing for medical research, will not only hasten this progress but also sustain and increase funding for taxonomy and biodiversity science research as a whole.

ACKNOWLEDGEMENTS

We thank all the volunteers and staff from the Australian Tropical Herbarium and the Adelaide lab that assisted with collection, voucher verification, preparation of samples, and/or provided assistance in the lab including Stuart Worboys, Caroline Puente Leliévre, Cameron Kilgour, Melissa Harrison, Martin Breed, and Kathy Saint. We also especially thank Maria Kuzmina and BOLD staff at the Canadian Centre for DNA Barcoding for their assistance with the sequencing.

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SUPPORTING INFORMATION

Figures S1-S4: Distance trees utilized for final results listed in Table S2. All phylogenies were inferred using the Neighbor-Joining method. The optimal trees or bootstrap consensus trees are shown with bootstrap support values. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Maximum Composite Likelihood method as implemented in MEGA5 and are in the units of the number of base substitutions per site. All positions containing gaps and missing data were eliminated. Separate *trnH-psbA* locus datasets for each family are compiled into two figures (S1-S2) and the final trees of the *rbcLa* + *matK* datasets are shown for the two study sites, Charmillan (Plot 1) and Koolmoon (Plot 2). The taxonomy of three species, *Pouteria euphlebia*, *Rhodamnia whiteana*, and *Waterhousea unipunctata* were corrected post analysis. Their formerly recognized names remain unaltered in the Figures. The updated names are listed in Table S1 and are as follows: *Pouteria euphlebia =Planchonella euphlebia*; *Rhodamnia whiteana = Rhodamnia costata;* and *Waterhousea unipunctata = Syzygium unipunctatum*.

Figure S1: Results with *trnH-psbA* for Elaeocarpaceae, Rubiaceae, Rutaceae, Sapindaceae, and Proteaceae.

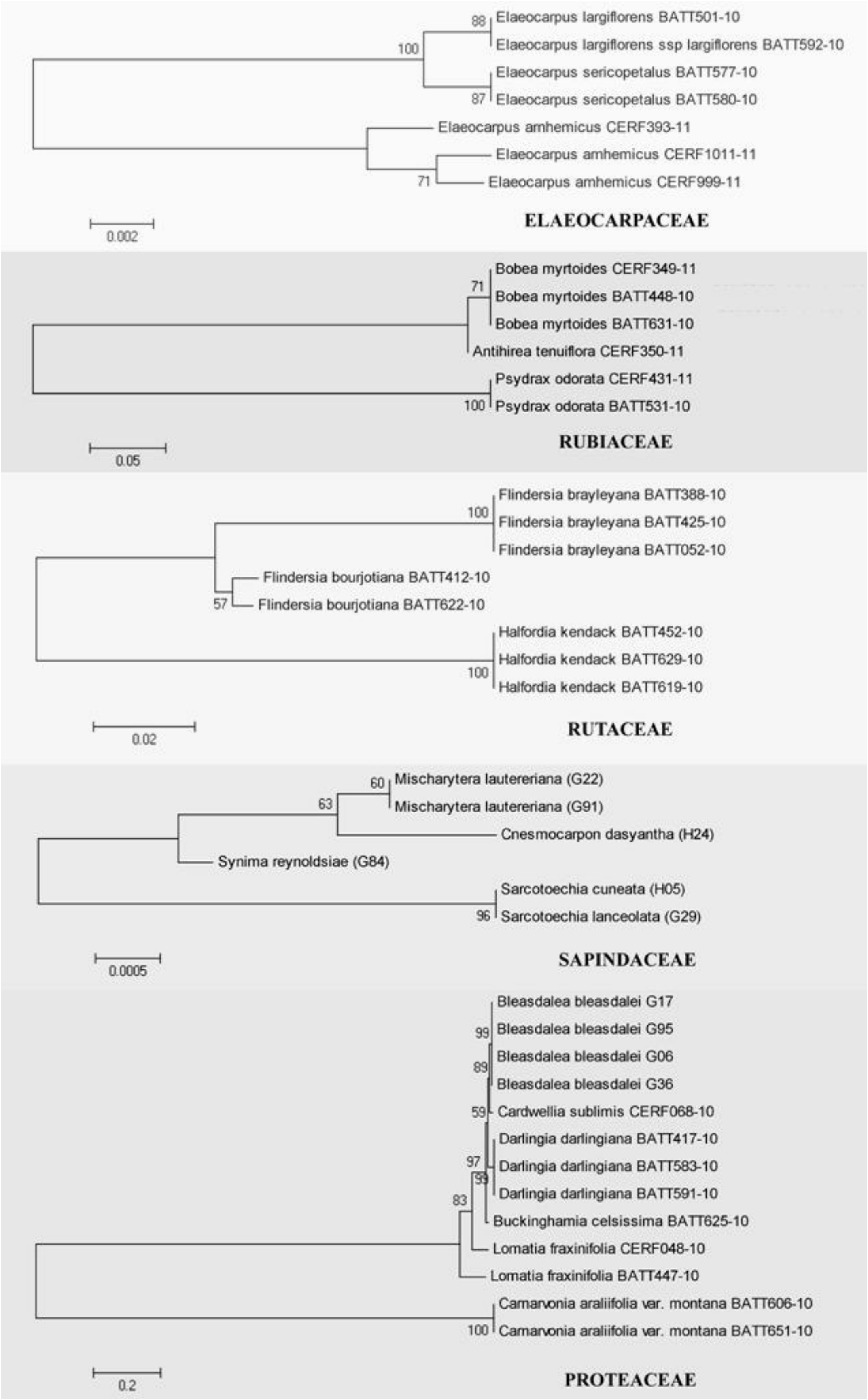


Figure S2: Results with *trnH-psbA* for Lauraceae and Myrtaceae.

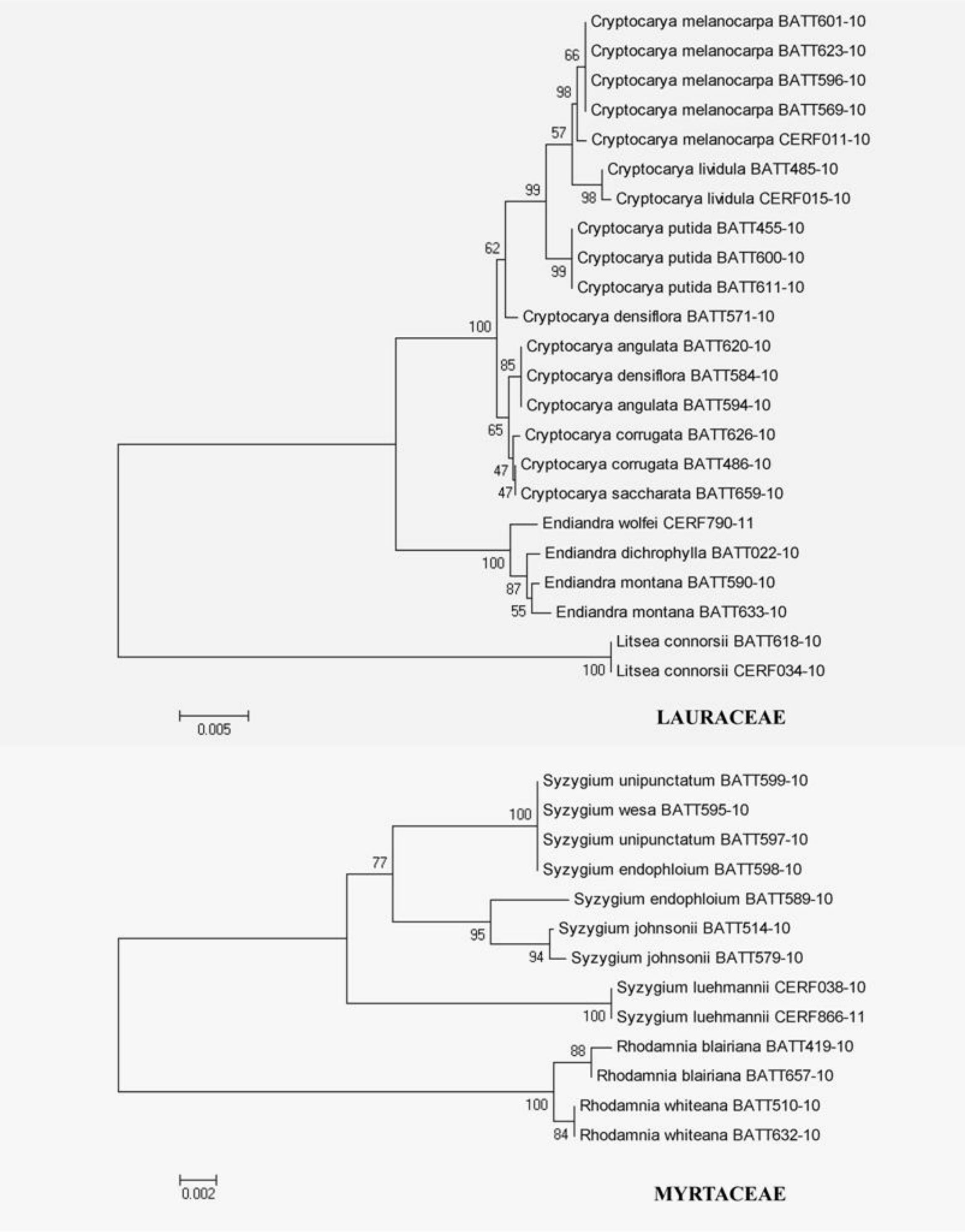


Figure S3: Charmillan plot results for *rbcLa* + *matK*

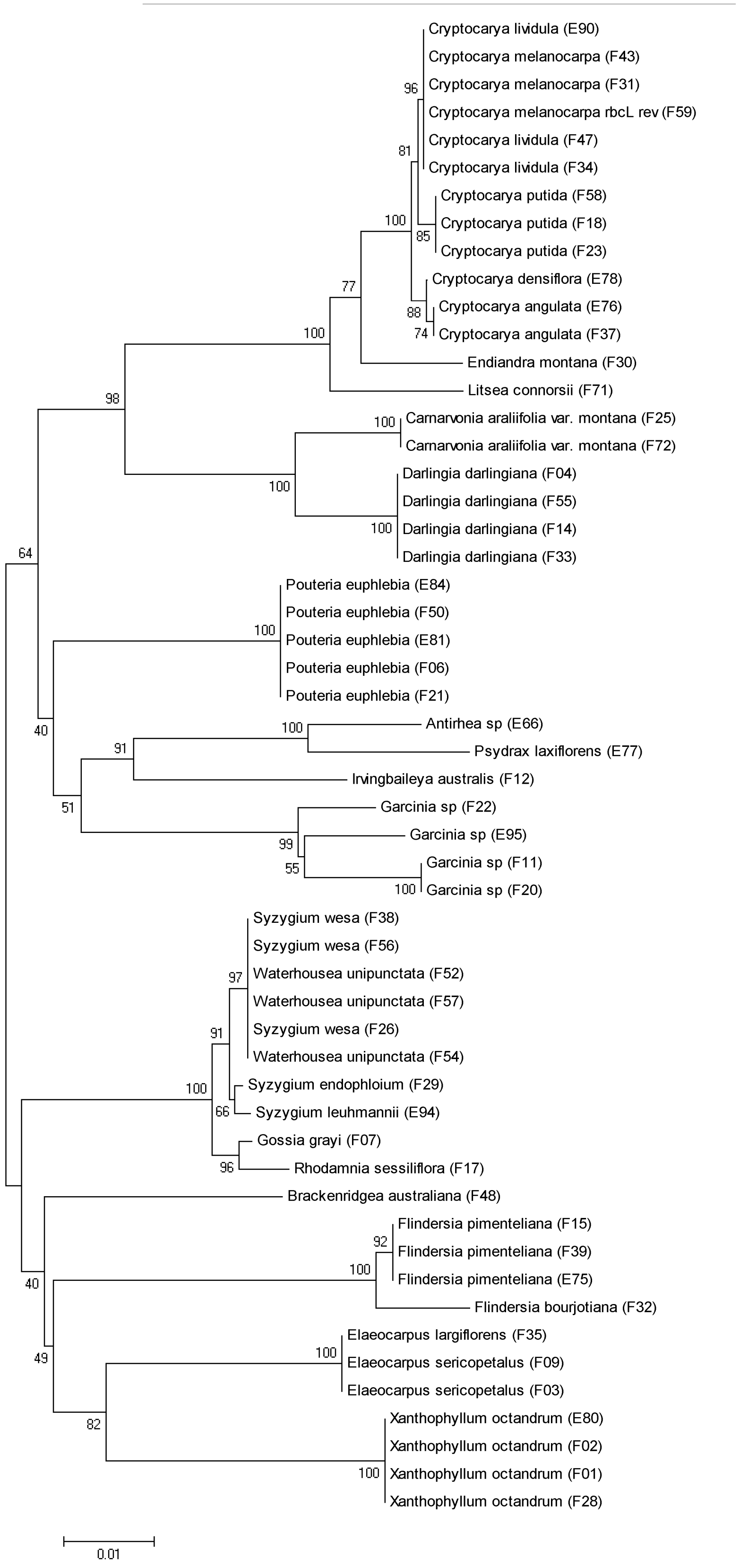
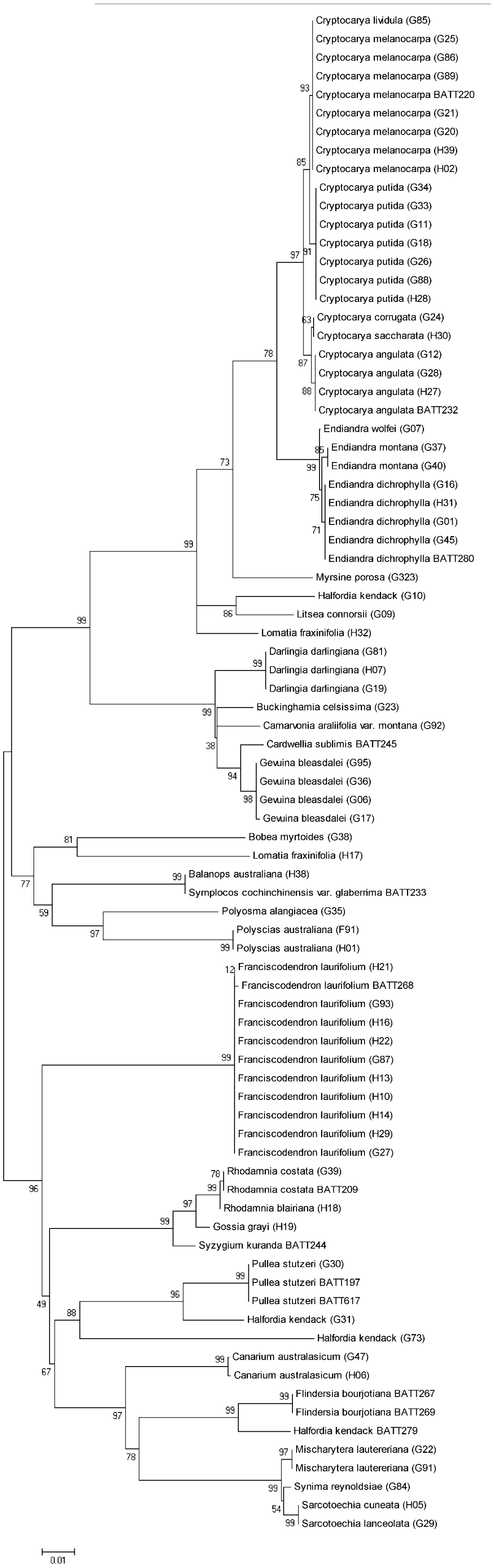


Figure S4: Koolmoon plot results for *rbcLa + matK*



PART II:

DIVERSITY PATTERNS IN WELL KNOWN FLORAS AND THEIR ROLE IN INFORMING CONSERVATION POLICY

CHAPTER 5

Linking park boundaries is not enough – A scientific assessment of the NatureLinks East meets west corridor strategy

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ABSTRACT

Aims & Methods A conceptual biodiversity corridor, the East Meets West area (EmW), has been established in South Australia by linking up existing reserves to focus biodiversity conservation activities. However, this precluded a comprehensive analysis of biodiversity value and threat status across the region, which is done here. Vascular plant, mammal, reptile and amphibian, and bird records from the Biological Survey of South Australia were analyzed separately for alpha and beta diversity patterns across the region of study. The observed biodiversity patterns were compared to existing reserve boundaries and the extent of native vegetation cover to assess the degree of threat and habitat connectivity.

Results Plant diversity and endemism is concentrated in the Mediterranean climatic zone to the south of the proposed corridor boundary, which also contains the most fragmented habitat and highest number of threatened plants. Vertebrate diversity is concentrated in the arid zone primarily to the northwest of the corridor boundary. Complementarity and alpha diversity analysis indicated that a high percentage of biodiversity from the bioregion is not represented within the proposed EmW corridor.

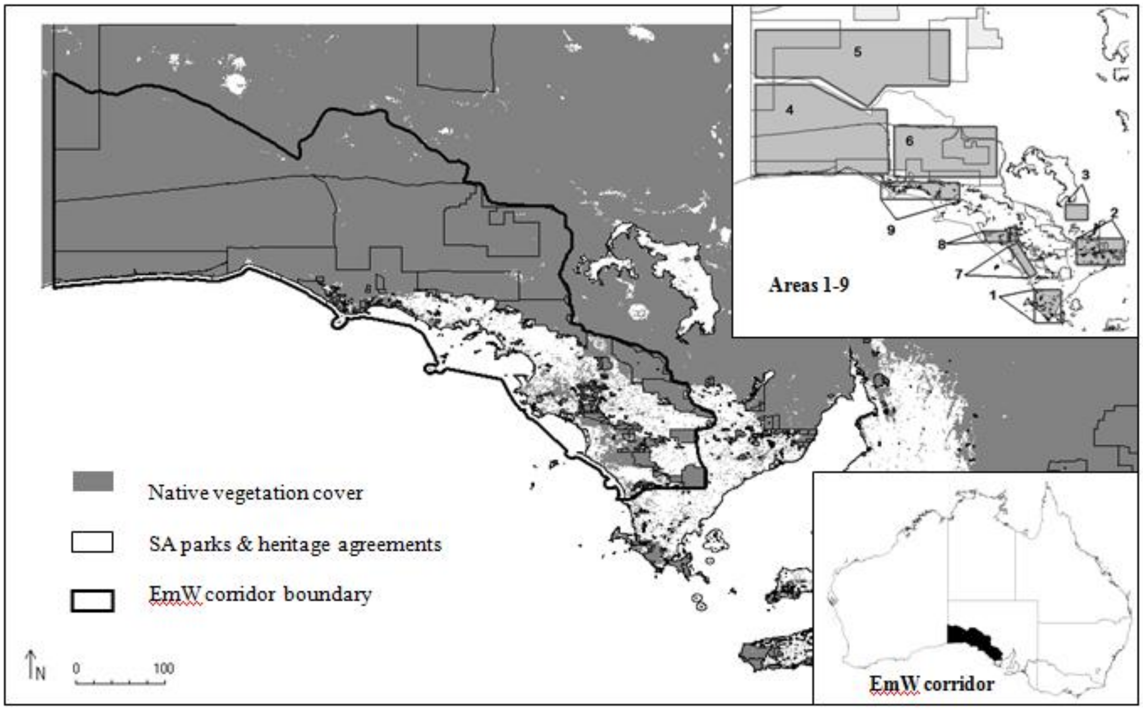
Main Conclusions Solely increasing connectivity between existing reserves may not be the best initial strategy for establishing biodiversity corridors. The current EmW corridor boundary does not incorporate a majority of the biodiversity assets of the region. A revised boundary is recommended to incorporate key biodiversity hotspots and refugia of relict and endemic species identified by this biodiversity analysis, improve biodiversity conservation outcomes, and incorporate off-reserve incentives.

INTRODUCTION

The importance of biodiversity corridors for conserving threatened species has become an increasingly relevant issue in Australia (Mackey *et al.* 2008; Dunn & Majer 2009; Doerr *et al*. 2010), as policy makers are faced with planning for climate change. Due to low altitudinal variation, climate change threats in Australia are particularly severe. Whilst much of the continent is predicted to become warmer, the picture for precipitation is much more variable (Hennessy *et al.* 2007). Overall South Australia is projected to become warmer and drier, which is expected to put much of its biodiversity and ecosystems under pressure (McInnes *et al.* 2003; Suppiah *et al.* 2006). The State of South Australia supports a high diversity of ecosystems and species of flora and fauna that are already considered threatened, and has one of the highest extinction rates in Australia (DEH 2002, 2007). In response to the increasing and synergistic nature of habitat and climatic threats, the South Australia Government has launched the Nature Links initiative (DEH 2007). Nature Links aims to establish five major biodiversity corridors across the State in order to incorporate all the major bioclimatic regions present. The boundary of the first area to be established, the East Meets West (EmW) area (DENR 2011; Figure 1), was drawn up to incorporate the predominant reserve areas in the west of the state (Eyre Peninsula to the border with Western Australia), and to potentially provide a linkage with conservation initiatives in Western Australia.

The reserve network in Australia has recently come under some scrutiny (Fuller *et al.* 2010), and although it is based on the principles of the comprehensive, adequate, and representative reserve (CARRs) system, (JANIS 1996), the reality of opportunistic land acquisition for conservation means that many ecosystems are poorly represented in the reserve system. Therefore the establishment of a biodiversity corridor based on linking up reserve areas may be missing important ecosystems or biodiversity hotspots in a region. This report assesses the conservation value and scientific underpinning of the EmW corridor by identifying areas of high biodiversity value within and adjacent to the boundary of the corridor. These areas are assessed and prioritized utilizing several criteria to help guide conservation efforts and planning.

Figure 1: East Meets West proposed corridor region (c) with native vegetation cover and park boundaries (a) and areas highlighted in results (b).



The data used for the analysis is from the Biological Databases of South Australia (BDBSA), a system established, maintained and populated by the South Australia Department of Environment & Natural Resources. The level of comprehensiveness of this biological survey is unparalleled in Australia. Currently over 3 million data records have been collected and databased, including information from over 20,000 vegetation and 5,000 fauna plots. Surveys began in 1971 and are still continuing today. The inventory sites are of the same, or comparable size, and the methodology has largely been kept standardized throughout (Heard & Channon 1997; Owens 2000), all of which render the dataset of world-class significance. Despite its noteworthy value, limited previous comparative analyses have been conducted on regions across the state using these data.

NatureLinks is a product of target 3.2 of South Australia's Strategic Plan and is considered a central component of the state's "No species loss nature conservation strategy" (DEH 2007). The NatureLinks initiative declares six operating principles as follows:

1. *Biodiversity conservation activities should be planned at landscape scale,*
2. *Habitat restoration should be undertaken at large spatial scales,*
3. *Species in fragmented landscapes should be managed as metapopulations (populations linked by the exchange of individuals),*
4. *An ecological community approach to biodiversity conservation should be encouraged,*
5. *Ecological restoration should be planned over long time scales, and*
6. *Biodiversity conservation activities should be underpinned by sound ecological knowledge.*

These six operating principles suggest that the corridor concept as defined by NatureLinks should function as both a corridor which functions to increase connectivity and a reserve which functions to increase representation. Here we argue that this is not achieved with the current EmW corridor plan and further more it does not uphold all of the six operating principles, particularly principles three and six. The types of analyses and assessments presented in this study are crucial to providing the information necessary for the state to meet its targets and to secure the integrity of South Australia's natural heritage. The South Australian biological survey dataset is distinguished and exemplar in this respect owing to the comprehensiveness of the survey and the standardization of the data collected from major phyla.

METHODS

Data collection

Data records for all native plants and terrestrial vertebrates from the Biological Survey of South Australia were extracted for the Eyre Peninsula and adjacent regions. A detailed manual outlining the methodology and data collection of both the vegetation (Heard & Channon 1997) and vertebrate (Owens 2000) surveys is available online. The data collected in these surveys form the basis of the biological databases of South Australia. These databases currently contain 730 datasets comprising 1.5 million vertebrate records, over 1 million flora location records, and over 11,000 photo points. This vast resource is periodically synthesized and published in conjunction with other State Herbarium and museum records to update the Census of SA Vascular Plants (Barker *et al.* 2005) and the Census of South Australian Vertebrates (Owens & Graham 2009) and represents the most comprehensive and authoritative biological dataset available for the region in the present study.

The raw data from the biological surveys was converted into shape files then imported into DIVA-GIS (Hijmans *et al.* 2005) software for analysis. The region was divided into 10 km^2 grid cells. The same grid cell alignment was utilized for all analyses presented in the results to enable cross comparison. Separate shape files were created for native plants, endemic plants, exotic plants, native vertebrates, native amphibians, native reptiles, native mammals, and native birds. These files formed the base layers for the analysis.

Data Analysis

Alpha diversity was measured with presence/absence data from the Biological Databases of South Australia and was measured separately for all classes of organisms across the entire study region; native plants, endemic plants, birds, reptiles and amphibians, mammals, and all vertebrates. Additional richness analyses were run for all state listed threatened plants, nationally listed threatened plants, threatened reptiles and amphibians, and threatened mammals and separate analyses were conducted for each of the nine areas listed in Table 1 and shown in Figure 1 for all vertebrates.

Beta diversity was measured using the Whittaker (1960) method; $\beta = (S/\alpha) - 1$ where S = the total number of species over the grid cells analyzed and α = the average number of species in the grid cells analyzed. Beta diversity was measured for native plants and endemic plants separately. Complementarity was measured using the reserve selection function in DIVA-GIS (Rebelo 1992, 1994). All records were weighted equally. No bias or "weight" was allocated to rare or threatened species. Reserve selection analyses were run for native plants, endemic plants, and all vertebrates. These analyses focused on identifying the maximum diversity that could be represented within the smallest number of locations and where these locations occurred in relation to the EmW corridor boundary.

Connectivity of the reserve network was assessed by creating shape files of the boundaries of all protected areas, state reserves, and Heritage Agreements (DEH 2008). High resolution data on the extent of native vegetation cover from the Biological Databases of South Australia (Figure 1) was also imported as a shape file for comparison to assess the degree of habitat fragmentation. This enabled interpretation of the biodiversity patterns with respect to current conservation policies and current land use management.

Table 1: Locality names of Areas 1-9 as shown in Figure 1

Area #	Locality/Reserve Name
1	Southern Eyre Hills
2	Northeastern Eyre Hills
3	Gawler Ranges, South Lake Gairdner
4	Nullarbor Plain
5	Maralinga Tjarutja Lands
6	Yellabinna-Yumbarra Reserves
7	West coast Eyre Peninsula block
8	Venus Bay-Calpatanna Waterhole
9	Ceduna Coastal Region

Sampling bias

Sampling intensity can bias biodiversity survey data if not enough sites are included or if the sites are not sufficiently distributed across the study region (Hortal *et al.* 2007). Although the survey utilized in the current study is considered exhaustive by global standards and thus less susceptible to common sampling biases a sampling bias test was run. The survey attempted to cover all major habitat types however some elements in the landscape were not sampled particularly for faunal biodiversity. A richness analysis was run on the number of surveys within each grid cell (Figure S1) and compared with the richness results from the species data.

Since the biological survey has been carried out progressively region at a time for nearly four decades there was also some question as to whether an analysis could be run comparing multiple regions across the state. The taxonomic change that has occurred within these respective regions over time could lead to a misrepresentation of species richness in the analysis. The data used for Eyre Peninsula sub-region however, has recently been revised and is considered up-to-date. A test was run to determine the degree of influence taxonomic change had on identifying important biodiversity areas. Both the original data set from the Biological Survey of Eyre Peninsula (2001-2005- see Brandle 2010) and the recently revised data set (2009) were analyzed separately and compared (Figure S2-5). This enabled a direct assessment on the suitability of analyzing the dataset presented in this study that spans four bioregions that were surveyed at different time periods between 1978 and 2008.

Site prioritization and recommendations

A system was devised to give a conservation priority rating for the sites highlighted by the results of this report. A total of nine areas were assessed (Table 1 and Figure 1). Each area was assessed against five different categories; biodiversity value, degree of threat, level of intact vegetation, relative connectivity, and the percent of the area that is already within a reserve or reserves. Each site was given a value for each of these categories then and the cumulative total for all values was used to produce a score or relative priority rating for future conservation efforts (Table 2). The values assigned to each category are qualitative. Biodiversity value was determined by reviewing the results from all the analyses in this study for each location. Areas with high diversity values for multiple taxonomic groups and/or analysis' were given higher ratings. Sites that were high for only one taxonomic group or fewer were given moderate or lower ratings.

Table 2: Biodiversity value and degree of threat prioritization scheme. Values 1-5 (e.g. Lowest to Highest) are qualitative. Columns two and three each represent two categories assessed using same scale. Maximum score equals 25.

Value	**Biodiversity & Threat**	**Intact Vegetation & Connectivity**	**Percent Reserved**	**Priority Level (Total Score)**
1	Lowest	Excellent	Highest	(1-5)
2	Low	Good	High	(6-10)
3	Moderate	Average	Moderate	(11-15)
4	High	Poor	Low	(16-20)
5	Highest	Poorest	Lowest	(21-25)

Degree of threat was based on two main criteria: (A) The closeness of the area to either adjacent degraded or non-degraded lands and (B) the richness of threatened species found in the area. A degradation index was developed based on native vegetation cover data (Figure 1). Areas mapped with completely intact native vegetation over large areas received “Excellent” ratings and areas severely fragmented with patchy intact vegetation received “Poor” ratings. Smaller areas that were partially cleared or partially fragmented were rated in the middle. Connectivity was based on how well connected the area was both (A) Internally, how well connected the reserves/intact areas were within the area and (B) Externally, how well connected these areas were to other reserves/intact areas in adjacent areas and the larger reserve network represented by the EmW corridor. Percent reserved was defined by a rough percentage of how much of the highlighted area occurred within a current reserve or heritage boundary.

RESULTS

The region of study is shown in Figure 1, with native vegetation cover layer, park boundaries, and the EmW corridor boundary. The upper right inset map in Figure 1 shows nine areas for which the results were analyzed in depth and are referred to throughout the text. Large-scale habitat fragmentation is evident in Figure 1 throughout the southern parts of the Eyre Peninsula in the Mediterranean zone whereas the arid zone shows less evidence of vegetation clearance and fragmentation. A map of all the biological survey sites from the region from which data was utilized for the analysis is provided in the supplementary info (Figure S6).

Plant diversity patterns

A clear correlation between richness of native plant species across the EmW region (Figure S7) and richness of endemic plants (Figure 2) was observed. Both share a similar pattern of hotspots in the southern tip of the Eyre Peninsula and higher diversity in the Mediterranean than in the arid portions of the EmW area. An exception to this trend is a hotspot in the Yellabinna Regional Reserve (Area 6), with a diversity measure of 235 native plant species. This is the second highest value for the region, by only one species. Moderately high levels of diversity occur in the NE Eyre Hills region (Area 2), east of the EmW corridor, and to the west within the corridor in the Pinkawillinie, Cocata, Kulliparu, Venus Bay, and Calpatanna Waterhole Reserves (Area 8). Moderate levels of diversity are observed through the Yellabinna Reserve region (Area 6) into the Maralinga Tjarutja Lands (Area 5). Very low levels of diversity are observed in Area 4, the Nullarbor reserves.

Figure 2 shows the richness of endemic plant species across the region. The southern region of the Eyre Peninsula (Area 1) is clearly the main hotspot of endemism in the whole study area. This is also notably the wettest part of the entire region (Schwerdtfeger 1985). Many of the plants that occur there only occur in the Eyre Peninsula (Lange & Lang 1985; DEH 2002; Pobke 2007). There are two additional areas with moderate levels of endemism, the northeastern Eyre Hills (Area 2), east of the EmW corridor boundary, and the area surrounding and east of Port Kenny (Area 8). The majority of the remaining region has relatively low levels of plant endemism. Area 4, the Nullarbor plains, notably has virtually no endemic plants.

Figure 2: Endemic plants diversity and complementarity in relation to corridor boundary.

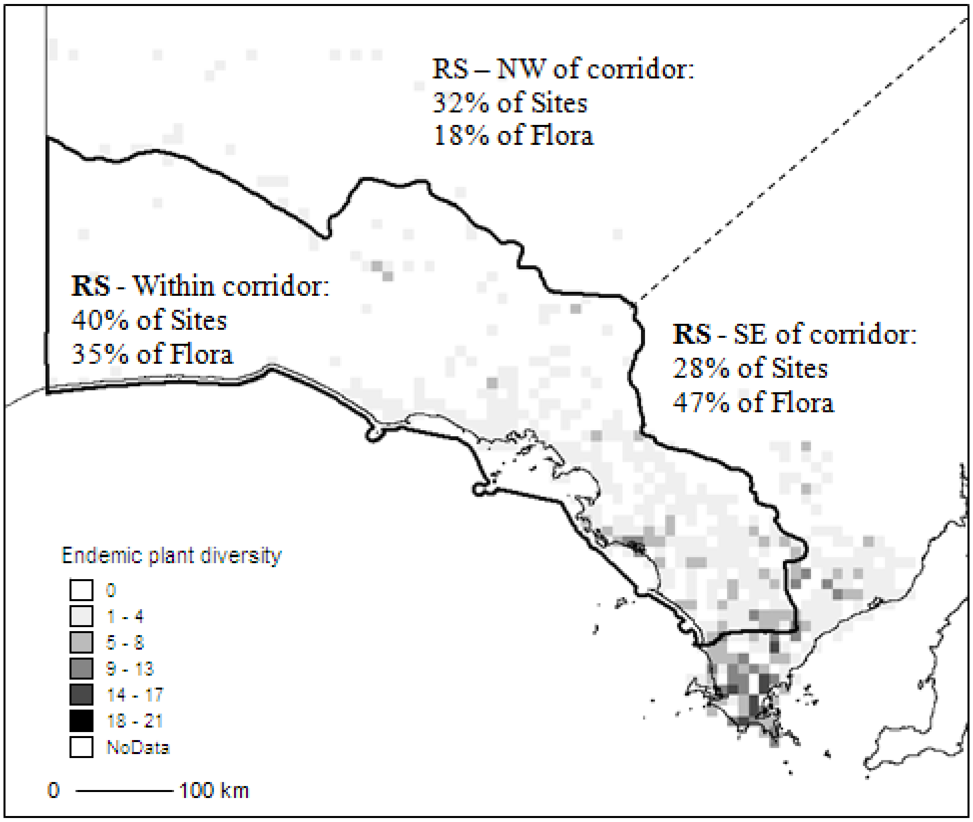


Figure S8 shows the distribution of all state listed threatened plants in the EmW corridor region. Nearly all of the threatened plants from both categories, Vulnerable and Endangered, are clustered within Areas 1 and 8. A similar pattern was found for all nationally listed endangered plants. All nationally listed endangered plants occur in Area 1, south of the EmW corridor boundary. Nationally listed vulnerable plants are clustered into three main localities; the southern Eyre Hills (Area 1), the Venus Bay to Streaky Bay region (Area 8), and along the Ceduna coastal region (Area 9).

Patterns of beta diversity, or turnover, for plants (Figure S9) exhibited a similar pattern to endemic species richness. High beta diversity is observed in the southern and eastern Eyre Peninsula outside the EmW boundary (Areas 1 and 2) and within the EmW corridor boundary at two localities, the Yellabinna reserve (Area 6) and the Venus Bay area (Area 8). The northwestern part of the EmW corridor, the Nullarbor Plain (Area 4), is notable for its very low turnover value, and indicates a low diversity of habitats and/or species assemblages in the region.

Complementarity results (Figure S10) generated from the reserve selection (RS) analysis for native plants are summarized in Figure 2. A total of 1,693 unique taxa were identified in this analysis out of the 100 sites selected within the EmW bioregion. Figure 2 divides the study region into three main areas, within the EmW corridor, northwest of the corridor (Area 5), and southeast of the corridor (Areas 1, 2, and 3). A total of 60% of the sites selected in the RS analysis occur outside the corridor boundary to the northwest and southeast. These sites represent 65% of the flora of the entire region. This means that if only these sites were protected, 65% of the entire region's plant diversity would be represented. A total of 47% of the flora, nearly half, is represented in the southeastern region. Only 40% of the sites prioritized by the reserve selection analysis occur within the EmW corridor. The most important areas of complementary diversity are in the southern Eyre Hills (Area 1) and the Yellabinna Regional Reserve (Area 6). Thus protecting only these two sites would give the highest representation of both the Mediterranean and arid floras for the smallest area.

Vertebrate diversity patterns

Table 3 provides a summary of diversity patterns observed for vertebrate groups. Complete results for each vertebrate group are provided in the Supporting Information (Figures S11-13). Low diversity of reptiles and amphibians is observed in the southern part of Eyre Peninsula but diversity increases to the northwest. Hotspots are concentrated in the arid zone, occurring in Yumbarra and Yellabinna reserves (Area 6), and highest in the Maralinga Tjarutja Lands (Area 5). This area is known to have one of the richest reptile faunas in Australia (Pianka 1984: Morton & James 1988, Foulkes & Thompson 2008). A similar pattern is observed for native mammals. Low diversity values occur in the Mediterranean region, with the exception of one area, the northeastern Eyre Hills region (Area 2). This locality is unique in having high diversity, surrounded by a large region of low diversity. Two significant hotspots occur within the proposed corridor region, in the Yellabinna Reserve (Area 6). The results for the Maralinga Tjarutja Lands (Area 5), and the adjacent region, are congruent with the reptile diversity results. This area as a whole has the highest levels of mammal diversity across the entire area of study.

Table 3: Areas of native vertebrate species diversity when analyzed by class

Area #	Reserve/Region Name	Total spp.	Avg. spp./10 km²
Amphibian and reptile diversity hotpots			
5	Maralinga Tjarutja Lands	84	12
6	Yumbarra-Yellabinna	78	12
Mammal diversity hotspots			
2	Northeastern Eyre Hills	18	3.7
5	Maralinga Tjarutja Lands	26	6
6	Yumbarra-Yellabinna	21	5
Bird diversity hotspots			
3	South of Lake Gairdner	88	38
2	Northeast Eyre Hills	88	30
7	Bascombe Well	91	29
5	Maralinga Tjarutja Lands	90	26
6	Yumbarra-Yellabinna	103	25

Bird diversity levels are more equal across the region than other vertebrates, and no consistent bias between arid and non-arid zones is evident. High levels of diversity are specific to habitats in smaller areas rather than larger bioregions or sub-regions. The area near Lake Gairdner, (Area 3), has the highest level of diversity per grid cell. This area contains 88 species, 51% of the total bird fauna. Areas of comparable size were compared across the EmW region for total species richness. The results for all areas were similar (Table 3). However average diversity of species per 10 km² within these areas varied substantially. Moderate levels of bird diversity are observed in the northeastern Eyre Hills (Area 2), the Bascombe Well Reserve (Area 7), Yumbarra-Yellabinna reserves (Area 6), and along the northwestern EmW corridor boundary between Area 4 and 5.

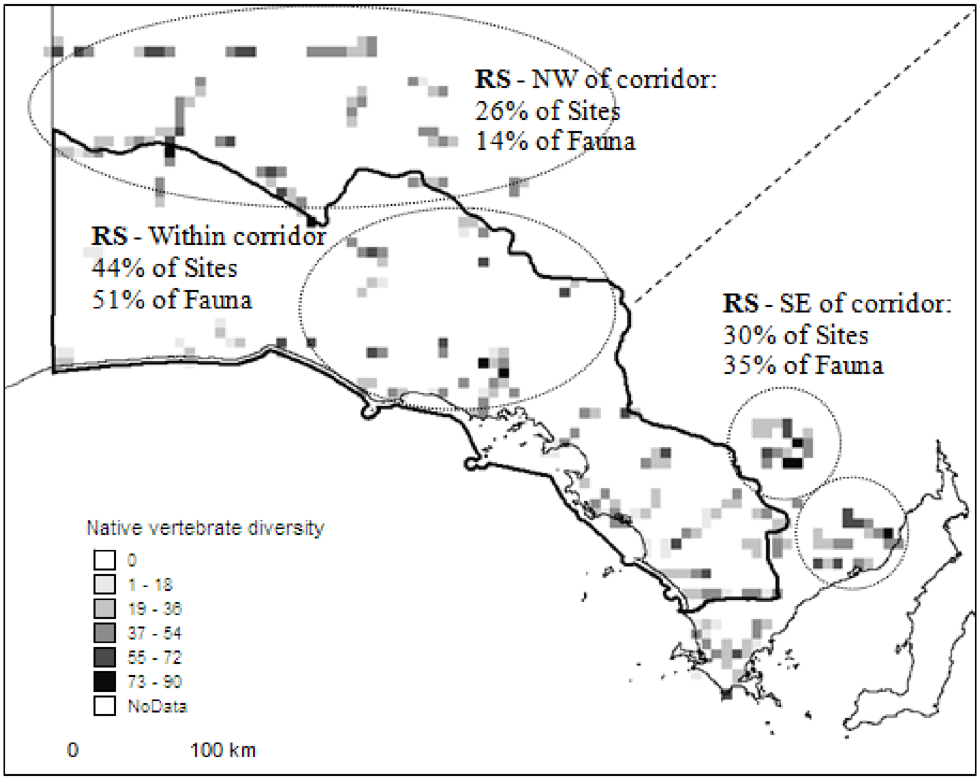
Richness of all vertebrates combined is shown in Figure 3.The most diverse areas (circled) contain at least one hotspot area containing 73-90 species (dark black) and are surrounded by moderately high diversity areas containing 55-72 species (dark grey). A summary is provided in Table 4. The Maralinga Tjarutja Lands (Area 5) have the highest alpha diversity levels in the study area. Area 6 has moderate diversity levels in all groups, whereas Areas 2 and 3 are significant primarily due to high levels of bird diversity.

Table 4: Sites with highest overall vertebrate species diversity and the relative richness of each major class

Locality		**Alpha Diversity Level**		
Area #	**Region/Reserve Name**	**Rept./Amph.**	**Mammal**	**Bird**
2	Northeastern Eyre Hills	Low	Low-Mod.	High
3	South of Lake Gairdner	Low	Low-Mod.	High
5	Maralinga Tjarutja Lands	High	High	Moderate
6	Yumbarra-Yellabinna	Mod-High	Moderate	Low-Mod.

Complementarity of all native vertebrates revealed a roughly 50/50 proportion of representation of sites prioritized and species represented within and outside the EmW corridor (Figure 3). The areas selected by the reserve selection analysis are clustered in Areas 1, 2, 3, 5, 7, and 8 (Figure S14). The highest ranked site occurs on the border of the EmW corridor between Areas 4 and 5, which is the ecotone between the Nullarbor and Great Victoria Desert Bioregions. The second highest ranked site occurs in the southern Eyre Hills (Area 1). This pattern of clustered sites identified in these particular regions is congruent with the complentarity results for plants. It is also similar by having very poor site prioritization in the Nullarbor region.

Figure 3: Native vertebrate diversity and complementarity in relation to corridor boundary.



Summary of diversity patterns

High levels of both alpha and beta diversity are observed in the southern portion of the Eyre Peninsula which is within the Mediterranean bioregion, and the area of highest rainfall. This area also has the highest endemism and number of threatened plant species. These results strongly contrast with the patterns observed for vertebrate species. High levels of diversity for vertebrates are more prevalent in the arid zone, particularly the Maralinga Tjarutja Lands (Area 5) and the area around Lake Gairdner (Area 3) for birds.

Complementarity analyses for the region prioritize sites clustered in three main areas: north of the EmW corridor boundary in the Maralinga Tjarutja Lands region (Area

5), the southern portion of the EmW corridor (Areas 7 and 8), and the area to the south and east of EmW boundary (Areas 1, 2, 3). The results of the reserve selection and alpha diversity analyses indicate that a high percentage of biodiversity of the study area is not represented within the EmW corridor.

Habitat fragmentation and the existing reserve system

Assessing how well the observed biodiversity in the study area is represented within the existing reserve network (Figure 1), and the degree of connectivity between key biodiversity areas was considered a crucial component to this study. Table 5 summarizes the assessment of all nine areas analyzed in the study region. A linked network of reserves with intact vegetation is evident along the northern boundary of the EmW corridor. However a large cleared area separates Areas 7 and 8 from this northern intact region. A matrix of cleared land also extends into Areas 1 and 2 that have been shown to have high biodiversity values. Both of these areas are disjunct from the main corridor reserve system. They are also significantly isolated and highly fragmented, surrounded by agricultural lands (See Figure 4 inset).

Table 5: Results of prioritization scheme for Areas 1-9

Area	**Biodiversity Value**	**Threat**	**Intact Vegetation**	**Connect-ivity**	**Percent Reserved**	**Score**	**Pri-ority**
1	Highest	Highest	Poorest	Poorest	Lowest	25	**1**
2	High	High	Poor	Poor	Low	20	**2**
3	Moderate	Moderate	Excellent	Good	Lowest	9	**5**
4	Lowest	Lowest	Excellent	Excellent	High	6	**7**
5	High	Lowest	Excellent	Good	High	10	**4**
6	Moderate	Lowest	Excellent	Excellent	Highest	7	**6**
7	Low	Moderate	Average	Average	Lowest	15	**3**
8	Moderate	High	Poor	Poor	Lowest	20	**2**
9	Low	High	Average	Average	Moderate	15	**3**

Areas 7 and 8 also have low percentages of land represented in the reserve network. In Area 8, there is only a small percentage of native vegetation cover. There is a substantial block of native vegetation to the north of this area, however it is far from intact as much of it is used for grazing livestock (Brandle 2010). Area 7 stretches from the west of Bascombe Well, north to Venus Bay. This is the largest block of native vegetation in the Mediterranean region that is not within a reserve or Heritage Agreement area. Most of this area is not currently reserved and is used for livestock grazing (Brandle 2010). Area 9 has a network of reserves and heritage agreements along the coast, however the inland area is almost entirely cleared. Areas 5 and 6 are the most hopeful regions containing good biodiversity value and little evidence of habitat fragmentation. Area 4 is clearly intact, however has little biodiversity value.

Data limitations

The sampling bias tests showed no indication that sampling intensity biased the results, and there is no observable correlation between survey intensity and observed species richness (Figures S1 and S7). The test on the effects of taxonomic revision through time found that although some areas had slight changes in the number of species, the important areas identified in the analysis' for both the original and revised datasets were identical (Figures S2-S5). Thus whilst taxonomic update has a small numerical effect, it did not bias the analysis at the landscape scale. Other possible sources of bias include the seasonal conditions at the time the surveys were conducted (rain vs. no rain and spring vs. autumn) for both flora and fauna, under representation of cryptic species, and under representation of certain fauna groups such as snakes due to sampling methodology (Owens 2000). It is however unlikely that seasonal condition could account for much bias considering the sheer number of sampling sites across the study region and the patterns observed that correlate with climatic variables. Under-representation of some cryptic or faunal groups is also unlikely to have strongly affected the over-all diversity patterns.

DISCUSSION

The Nature Links initiative in South Australia is a strategy to influence the community and raise awareness of the importance of habitat connectivity. The East meets

West (EmW) corridor aims to utilize the existing reserve systems, link them up and incorporate them into a corridor. Thus the EmW corridor was defined on the basic premise that the parks in the region incorporate and represent the major biodiversity and ecosystems for the area. The bulk of the reserve lands on Eyre Peninsula were set aside because they were on un-alienated crown lands or of low agricultural value. Since the mid 1990's Parks have been acquired, according to the CARRs system of biodiversity criteria (JANIS 1996), but within the constraint of being restricted to areas that are for sale during annual funding cycles. Our analysis supports recent findings that the reserve system is missing major components of biodiversity and ecosystem representation in Australia (Fuller *et al.* 2010), and therefore a biological corridor strategy that solely aims to link up such reserves, may also fail to incorporate the major biodiversity and ecosystem variability in a region, as has been identified for the initial boundary delimitation of the EmW corridor.

The most important areas of floristic diversity and endemism for the region occur outside of the EmW corridor boundary in the southern Eyre Hills (Area 1). This region also contains the highest concentration of threatened plants, many of which are restricted to the region, and is one of the most fragmented landscapes in the bioregion. The CARRs criteria emphasize maximizing quality habitat with specific reference to rare species, areas of high diversity, endemism and/or inferred refugia, and that areas of such that are highly fragmented require integration into the overall conservation strategy. The EmW plan does not include this region, nor does it currently assess the pros and cons of and possible scenarios for creating linkages between it and other intact areas in the Mediterranean zone and is thus inconsistent with its own NatureLinks operating principle number three. Although the EmW plan is part of the State of South Australia's "No Species Loss" strategy (DEH 2007), it currently mainly links areas with low biodiversity values and low degrees of threat.

Our analysis of all major vertebrate groups also finds that important biodiversity assets also occur outside of the current corridor boundaries. The Yumbarra and Yellabinna reserves (Area 6), which occurs within the EmW corridor, has scattered localized hotspots for reptile and mammal diversity, however both faunal groups occur at consistently higher levels of diversity in the Maralinga Tjarutja Lands (Area 5) which is beyond the northern corridor boundary. This means that a national biodiversity hotspot for reptiles is excluded from the EmW plan. In addition the most important hotspot for bird diversity occurs around Lake Gairdner, in Area 3, which is also north of the boundary at its southeastern end. Our complementarity analyses indicate that for both flora and fauna, maximized complementarity gain is only achieved by incorporating additional sites (over 50% of the total) that currently occur outside the corridor boundary in adjacent areas (Areas 1, 2, 3, 5, 7, 8).

The purpose of a biodiversity corridor is not merely to link protected areas together but to increase the likelihood of survival of the species and habitats within the immediate bioregion of concern (DENR 2011, CCAD-UNDP/GEF 2002, Rosenberg *et al.* 1997). The usefulness of increasing connectivity between reserve areas as a null model for biodiversity corridor establishment or conservation success has also previously been called into question (Hodgson *et al.* 2009). Hodgson *et al.* (2009) highlight the uncertainty associated with increasing connectivity between areas without knowledge or reference to the species within them. They argue that better allocation of limited funds should focus on understanding species habitat requirements, population sizes, and conducting range shift modeling analyses, rather than efforts to simply increase connectivity between areas. Although the details of their arguments have been debated, there is a consensus that connectivity should not be the sole focus of conservation policy, rather investments should be based on critiques of their likely benefits (Doerr *et al*. 2011). Other researchers emphasize the importance of identifying refugial areas in Australia, which may contain relictual species (Morton *et al*. 1995; Moritz *et al*. 1997, Mackey *et al.* 2008). These areas having persisted through multiple and diverse climatic fluctuation in the past may provide more resilience to future climate change.

Many of Australia’s recognized biological refugia are not currently under any form of protection (Mackey *et al*. 2002). Analysis of the plant diversity results in the present study support notions from previous literature that the southern part of the Eyre

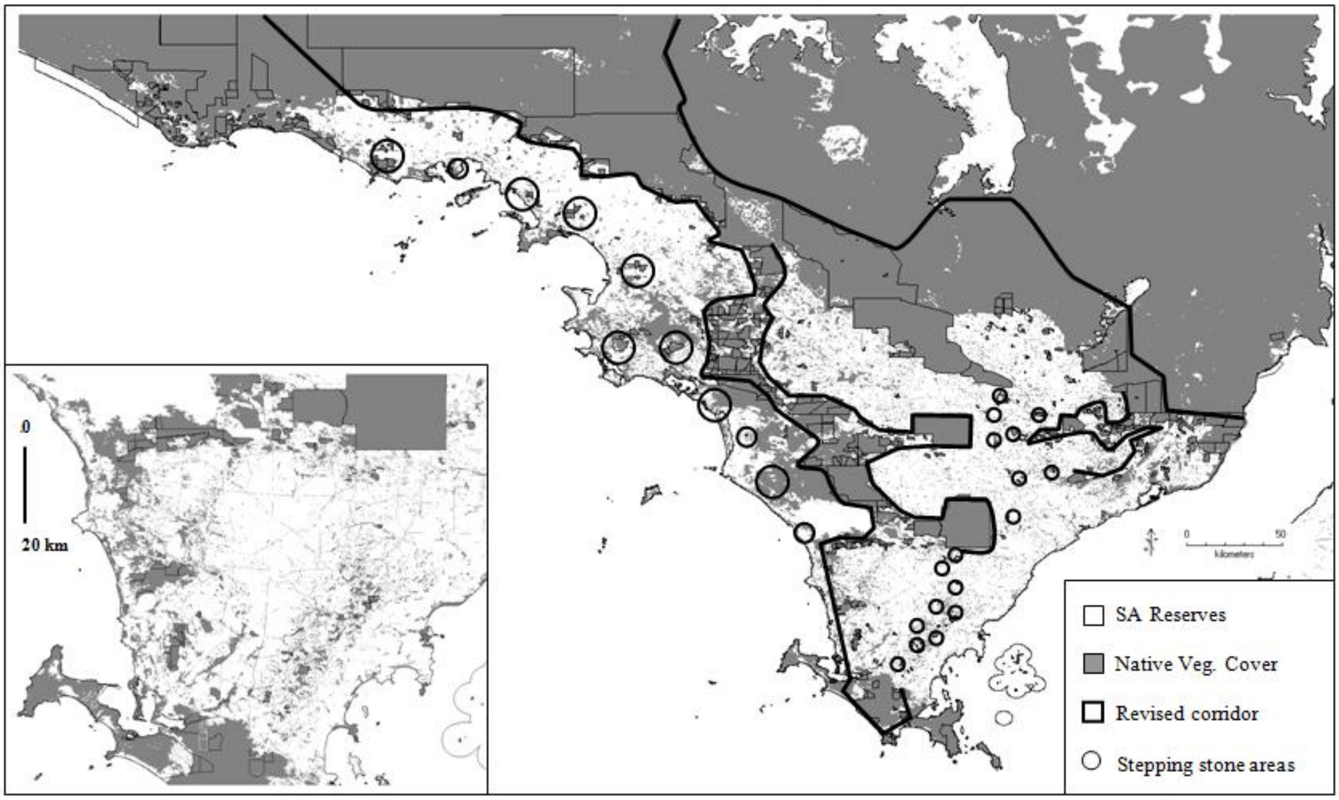
Peninsula forms one of these areas. The Eyre Peninsula in South Australia has been noted be an important refugium of a more mesic past supporting allopatric speciation and endemism (Tyler 1985; Main 1981; Koch 1977). *Echthrogaster,* a monotypic 'living fossil' beetle genus, is endemic to the Eyre Peninsula (Matthews 1985) and *Nothomyrmecia macropos,* the most archaic of all extant ant species (Taylor 1978), is only known from a confirmed existing population in the Eyre Peninsula and an unconfirmed location in Western Australia. Approximately 28 species of plants are also currently recognized as endemic to Eyre Peninsula (DEH 2002). If these hypotheses are true, then a strategy that ensures the integrity of this area may provide the most cost effective climate change mitigation conservation strategy. Neglecting this potential refugium could have disastrous consequences for species of concern. The capacity exists to simulate climate change and species range shift models to test these ideas, and is recommended as a next step.

The design of the EmW corridor preceded a thorough data analysis of the likely benefits to specific species occurring in the region and as a consequence the designation of the actual boundary lacks directly neglects NatureLinks operating principle number six which states that biodiversity conservation activities should be underpinned by sound ecological knowledge. Real conservation success is best achieved when quality biological data is available to inform subsequent actions, the current analysis serves as a recommendation based on quality biological data to modify the boundary of the EmW corridor (See Figure 4) to incorporate Areas 1, 5 and 3, and to omit Area 4 (the Nullarbor). For areas of high land value (around Area 1), we suggest that private land heritage agreements could be used to increase off-reserve conservation protection and to provide off-reserve stepping-stones that facilitate migration between reserves (see Figure 4).

Many of Australia's reserves have been established from lands residual to the interests' of agriculture, forestry, or other industries (Lindenmayer 2007, Mackey *et al*. 2008), and so linking such areas will not always be the best default basis for biodiversity corridor establishment, as has been found to be the case here for the EmW corridor. In addition, a number of areas acquired according to the CARRs principles within the EmW area, may be considered “underperforming protected areas” (Fuller *et al*. 2010), where more effort should be focused on areas with higher biodiversity value. For example the resources utilized to maintain and enforce reserve policy in the Nullarbor region (Area 4) may maximize gain if re-allocated to other areas prioritized in this analysis (e.g. areas 1, 5, 3).

Finally we re-emphasize here the world-class quality and standard of the Biological Survey Databases of South Australia data, which are the most comprehensive in the country, and a sound basis for future biodiversity corridor delineation. We conclude that increasing connectivity between existing reserves as an end in itself runs the risk of having limited conservation value without a robust species-based biodiversity analysis to underpin it. Biodiversity corridors should be designed based on the best available current species distribution data and preferably modeling of potential range shifts of selected key taxa relevant to the bioregion of concern. We also emphasize that it cannot be assumed that parks and reserves in Australia are fully representative of biodiversity and ecosystem variation in an area, and that bioregional conservation plans and corridor designs should re-assess the area of concern. In cases where these criteria haven’t been met, a re-allocation of reserve lands to areas that have higher biodiversity value and complementarity may provide part of the solution.

Figure 4: Revised corridor boundary that maximizes biodiversity value by adding stepping stone reserves (a). Area 1 is zoomed in (b) to show level of fragmentation.



ACKNOWLEDGEMENTS

We thank the South Australian Department of Environment and Natural Heritage and the University of Adelaide for providing funding for this study, the Biological Survey team that provided the data, and all those that encouraged our work.

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SUPPORTING INFORMATION

Figure S1: Number of surveys per grid cell (10 km²) across EmW region

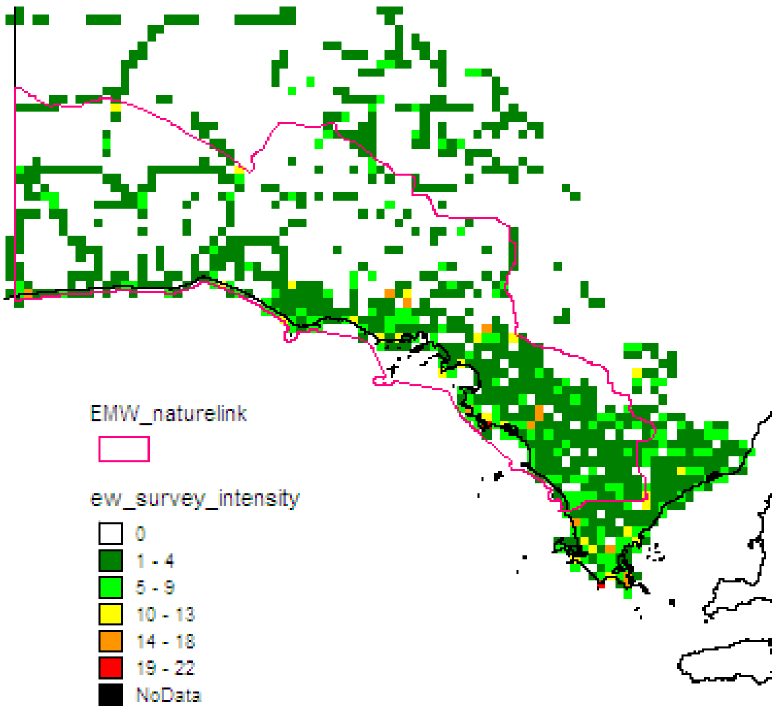


Figure S2: Richness of endemic plant species using un-revised data for Eyre Peninsula. Diversity values (No. of species) are inserted to the right of hotspot areas for comparison.

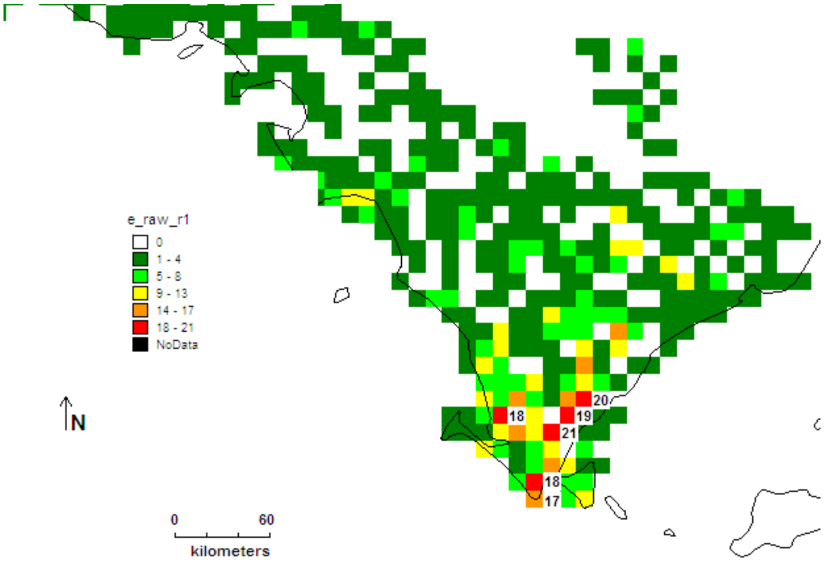


Figure S3: Richness of endemic plant species using updated taxonomy for Eyre Peninsula. Diversity values (No. of species) are inserted the right of hotspot areas for comparison.

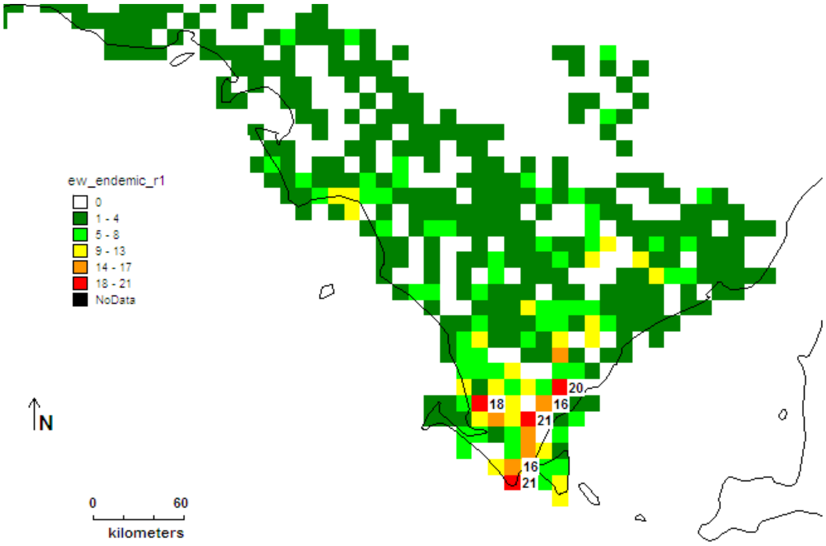


Figure S4: Richness of all native plants utilizing the old, un-refined dataset for the Eyre Peninsula (ranking of sites in order of highest diversity are noted to the right of hotspot areas in red, boundaries of SA reserves are overlaid).

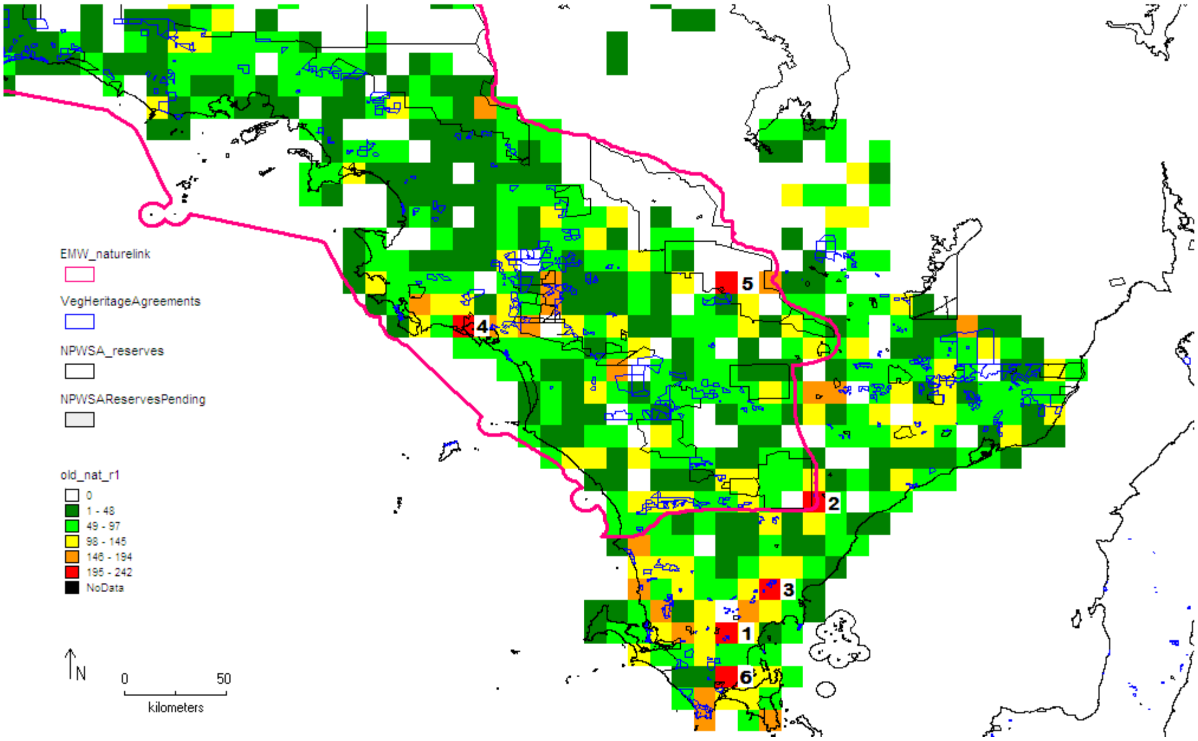


Figure S5: Richness of all native plants utilizing the updated taxonomy for the Eyre Peninsula (ranking of sites in order of highest diversity is noted to the right of hotspot areas in red, boundaries of SA reserves are overlaid).

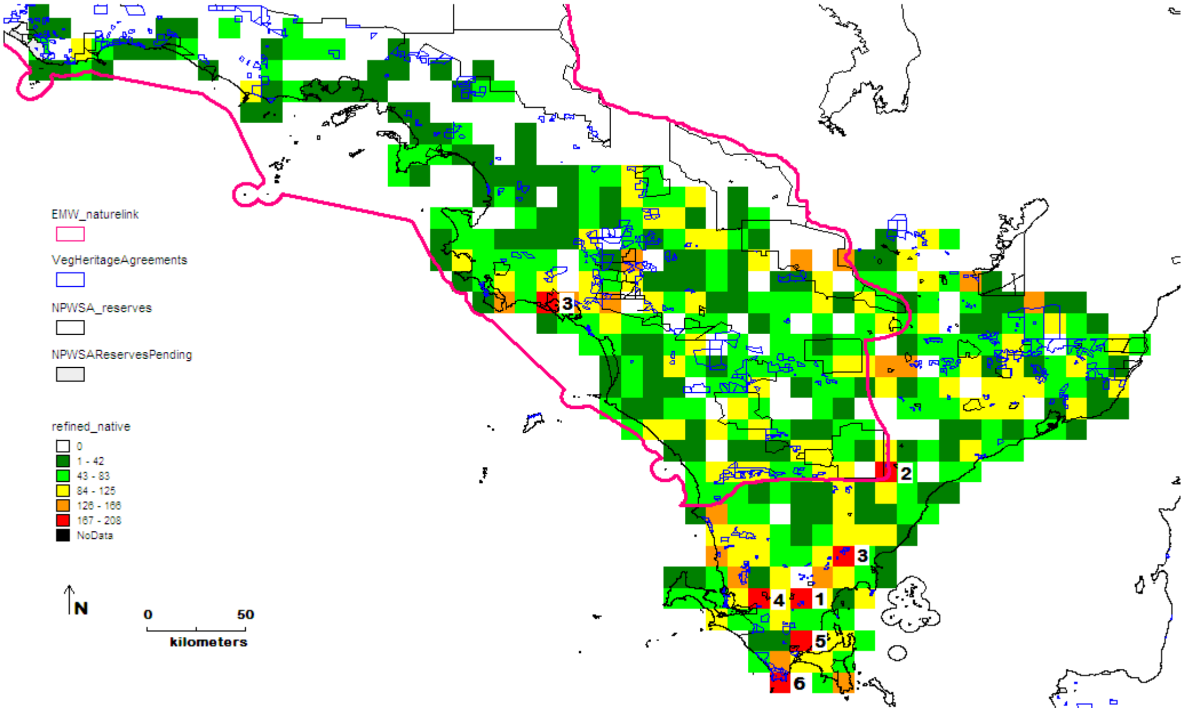


Figure S6: All survey sites from the Biological Survey of SA utilized for this study

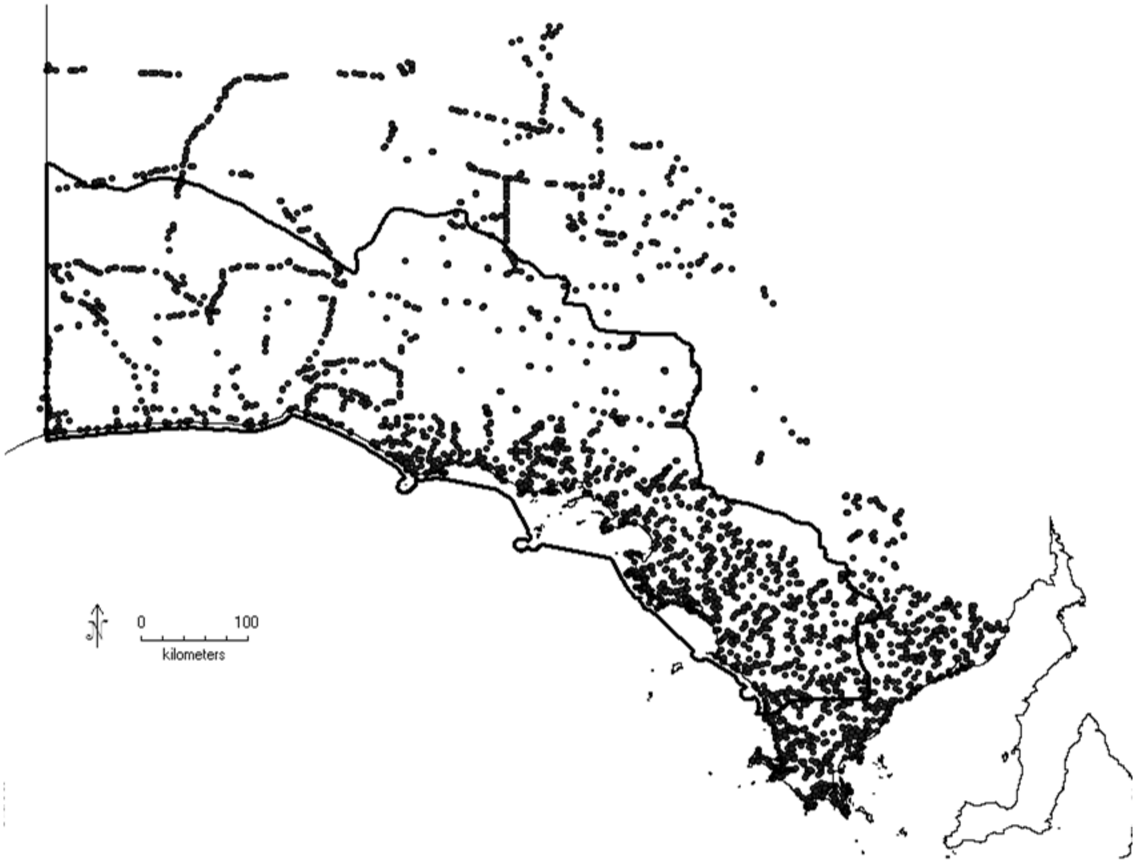


Figure S7: Richness of native plant species across the East Meets West region

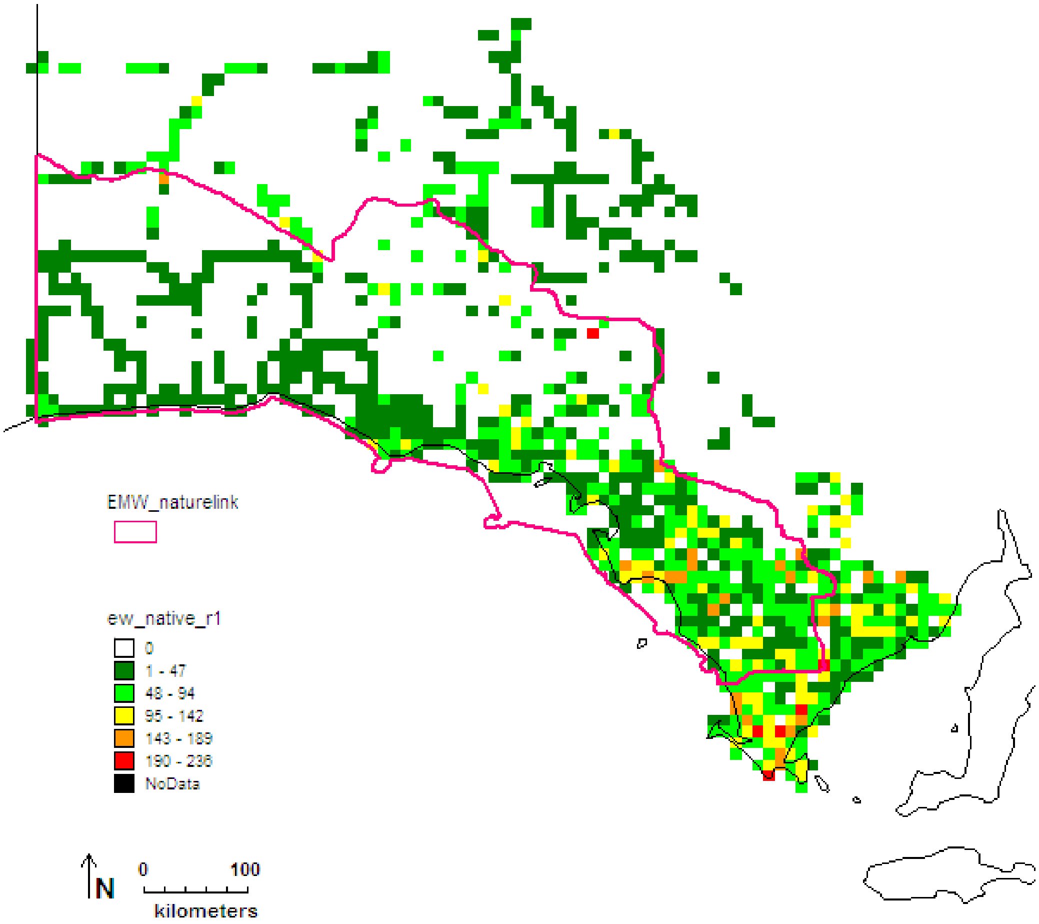
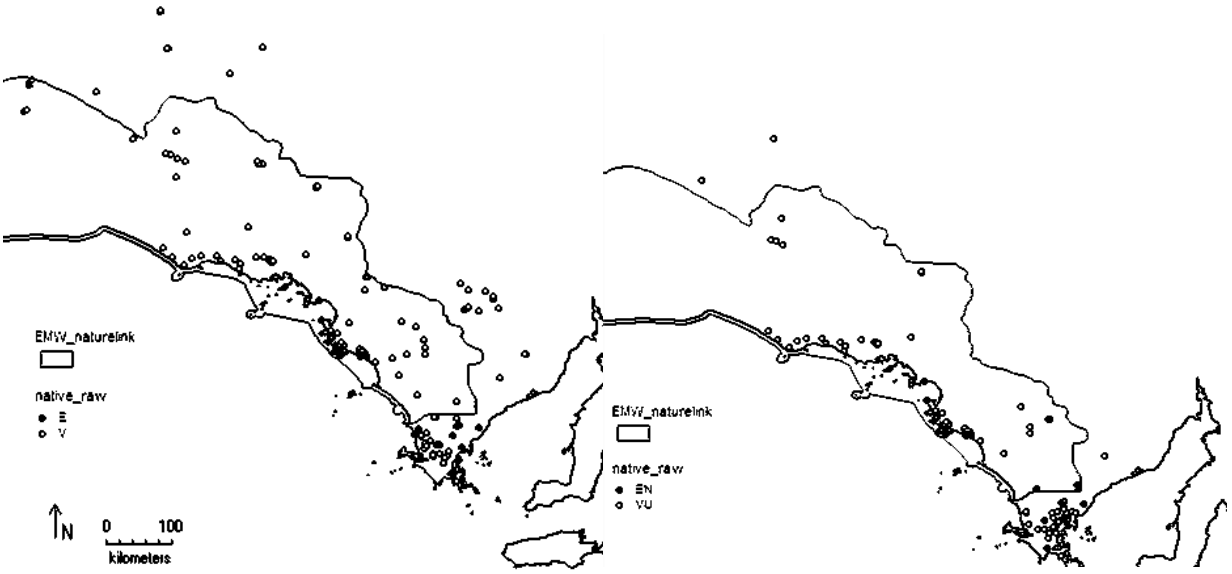


Figure S8: Distribution of nationally threatened plants, East meets West region. E = Endangered, V = Vulnerable



Nationally listed threatened

State listed threatened

Figure S9: Turnover of native plant diversity and endemic plant diversity (inset, upper right corner).

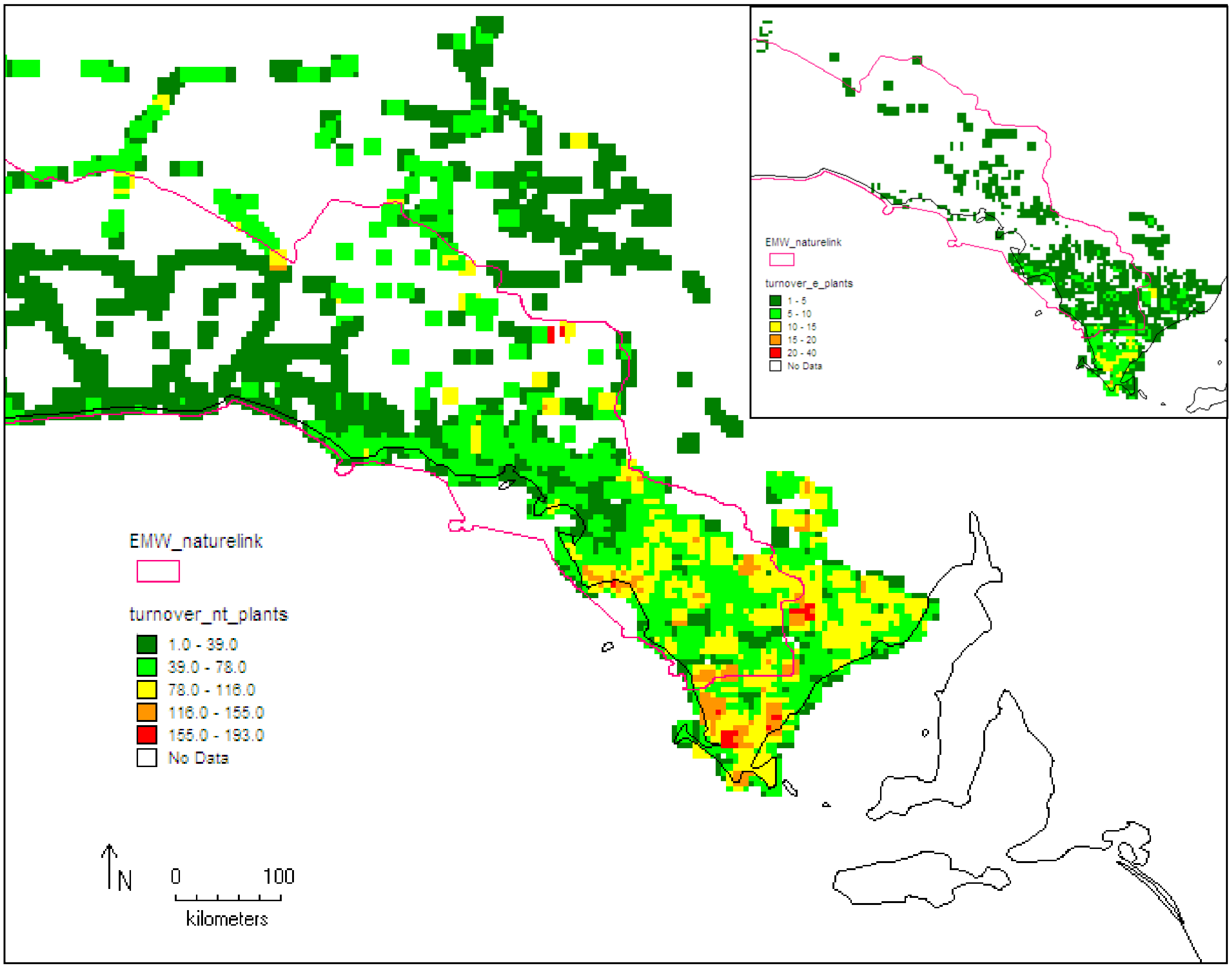


Figure S10: Reserve selection (complementarity) of native plants and endemic plants (upper right corner), East meets West region. Additional classes (legend) refers to number of unique species observed at each consecutive iteration of the analysis.

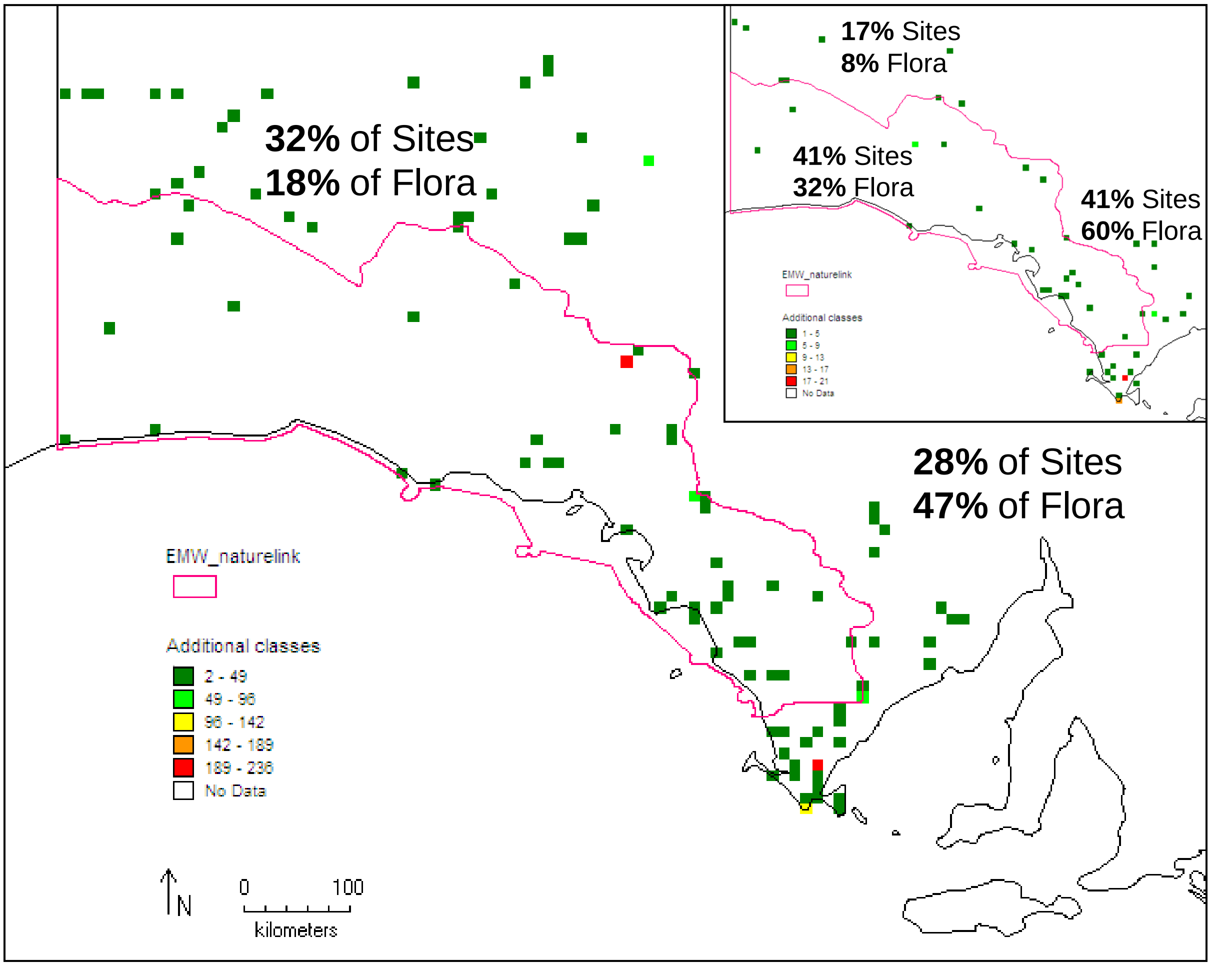


Figure S11: Richness of native reptile & amphibian species

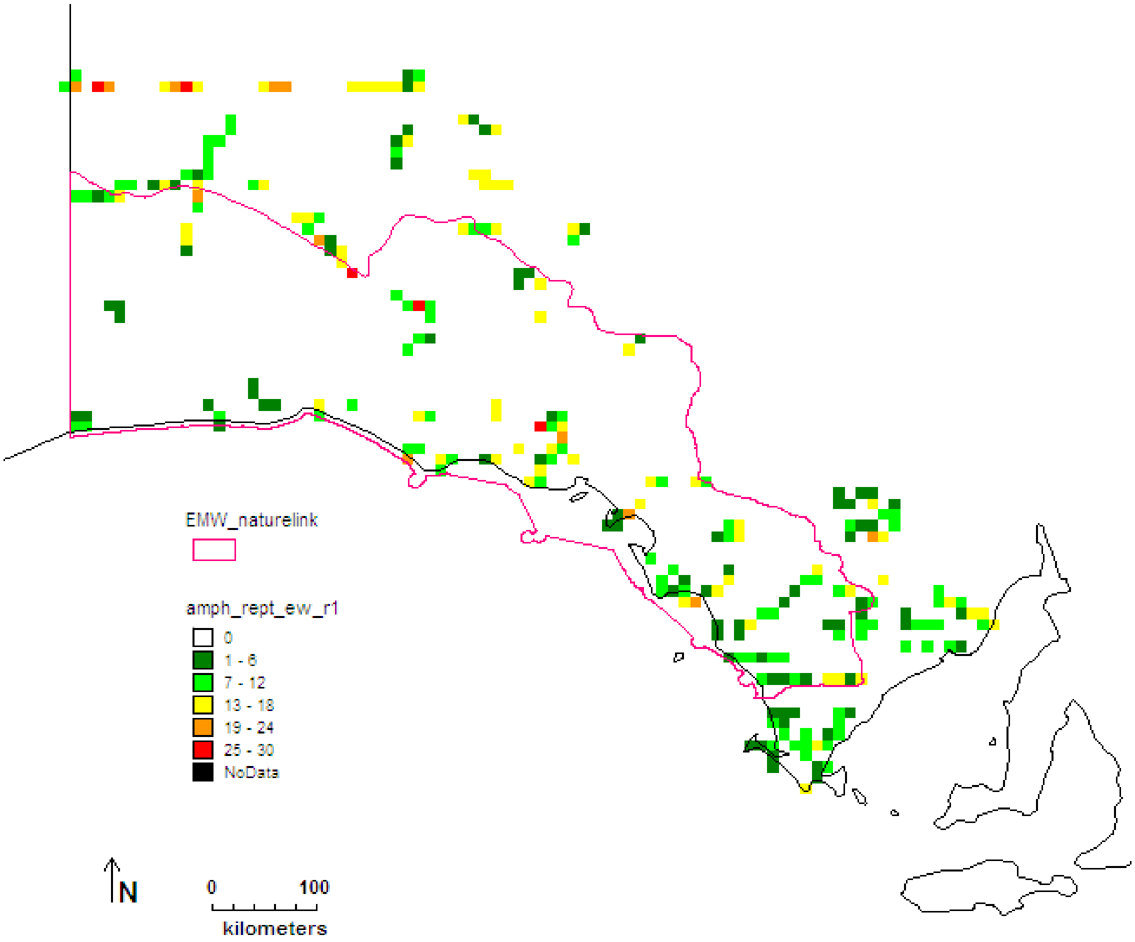


Figure S12: Richness of native mammal species

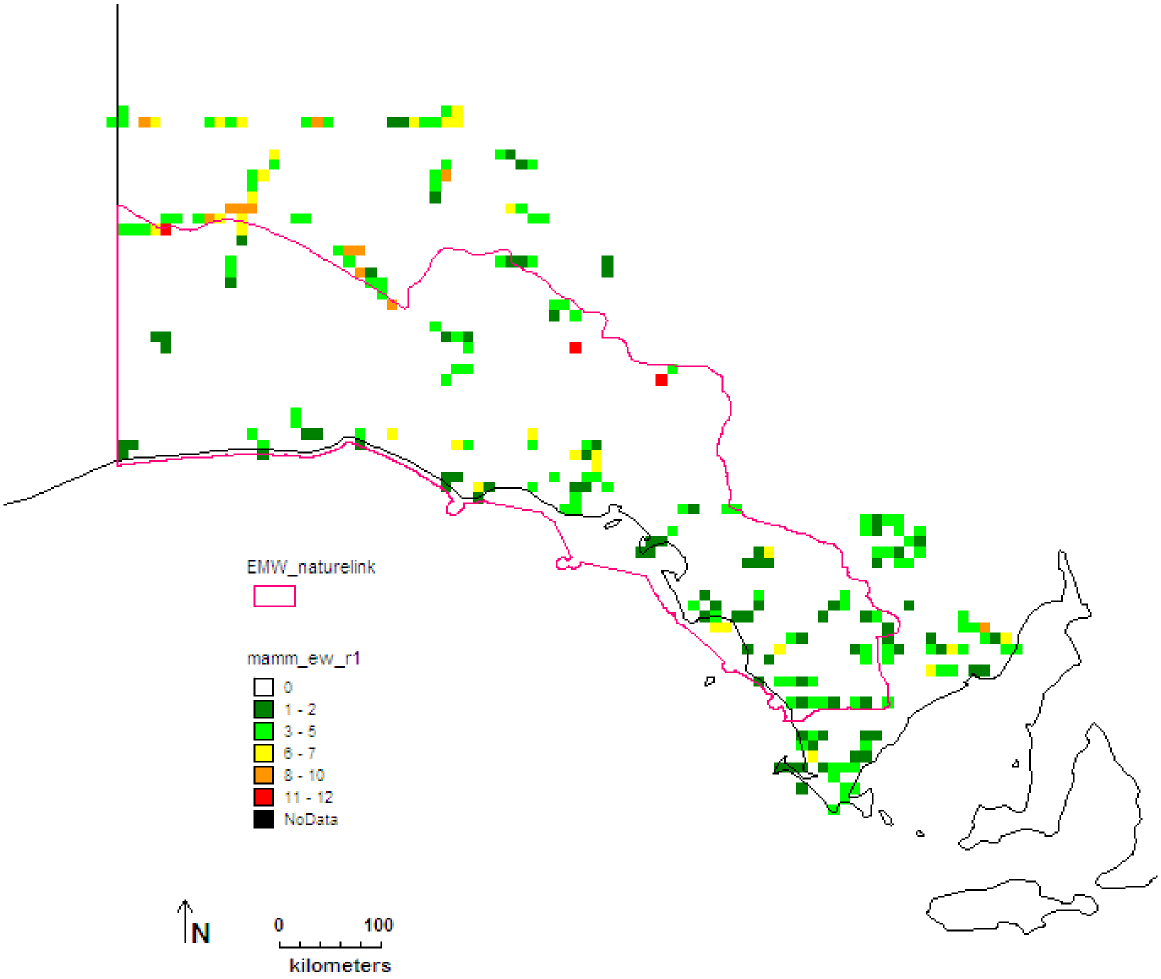


Figure S13: Richness of native bird species

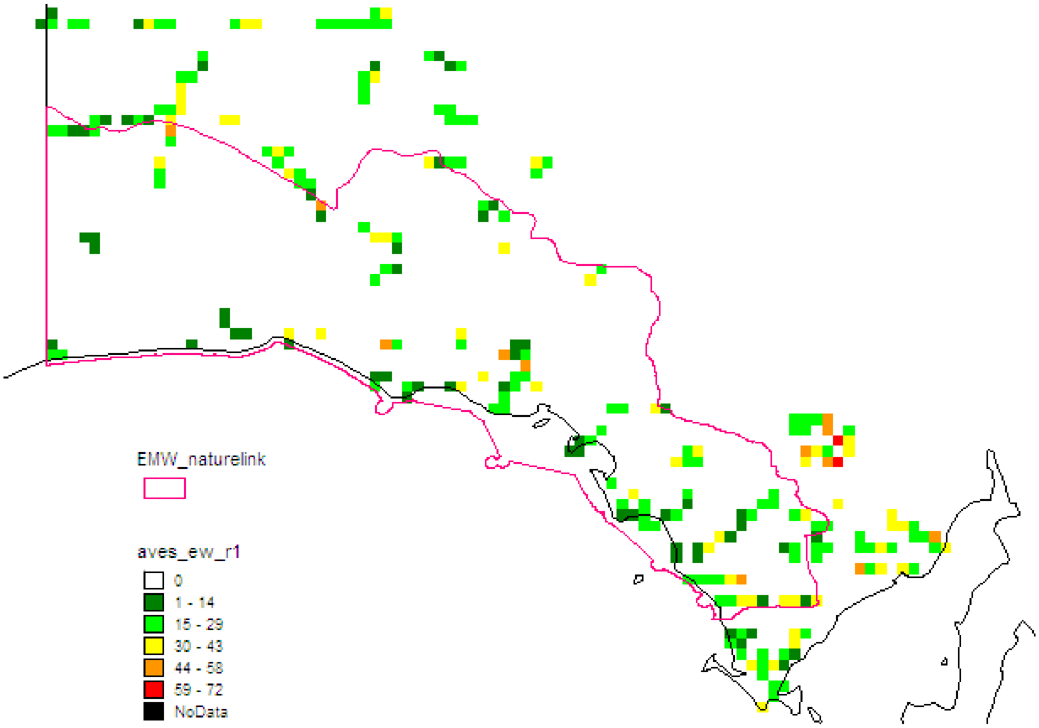
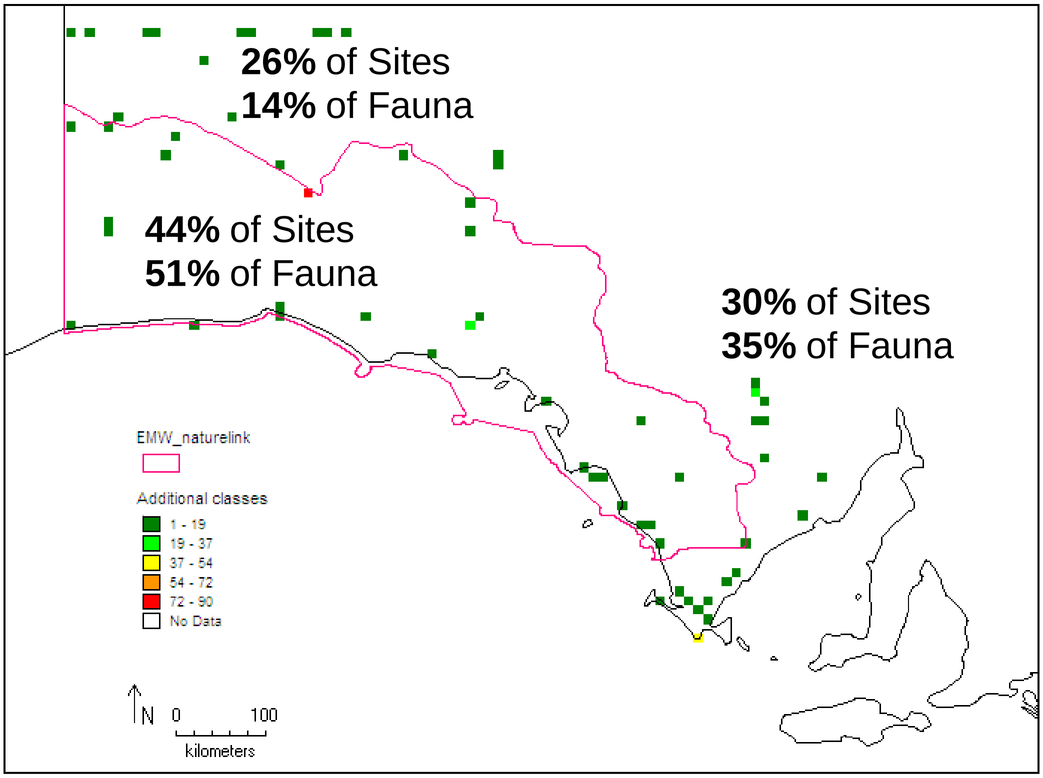


Figure S14: Reserve selection (complementarity) of native vertebrates



CHAPTER 6

Complex origins: Biome assembly and phylogenetic diversity in the Queensland Wet Tropics flora

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Draft submitted to Proceedings of the National Academy of Sciences, 07-2012

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Declaration of authorship

Conceptualization, data collection, and writing of this manuscript was carried out by the first author, Craig Costion. Will Edwards conceived and assisted with linear regression models and spatial autocorrelation analyses. Andrew Ford and Dan Metcalfe contributed the plant vascular survey dataset for analysis. Mark Harrington and Hugh Cross assisted with labwork, sequencing, and phylogenetic analysis. Darren Crayn and Andrew Lowe helped conceive and fund the project. James Richardson provided the dataset on floristic origins.

We hereby agree to the above and give permission for the inclusion of this manuscript in Craig Costion's doctoral thesis by publication:

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Date

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ABSTRACT

The relationship between phylogenetic diversity (PD) and genus richness (GR) is tested across a vascular plant dataset spanning the Queensland Wet Tropics bioregion. Phylogenetic diversity is measured from substitution rates of all angiosperm genera from the bioregion comprising the largest phylogenetic tree for a tropical biome to date. A linear correlation between phylogenetic diversity in genus richness is observed at four spatial scales however when the affects of genus richness are removed through linear regression a biogeographic pattern is unveiled which provides insight into the evolutionary history of the bioregion. Sites with higher PD than expected based on GR are directly correlated with sites that have a lower proportion of Gondwanan lineages and higher proportion of lineages that have dispersed to Australia from the Sunda plate in the last few million years. Lineages that have dispersed to Australia occur in higher proportions in the lowlands of northeast Queensland mostly below 200 meters suggesting that phylogenetic niche conservatism has played a role in enabling lineages to establish in Australia's extant rainforest refugia of relict Gondwanan affinity.

INTRODUCTION

The Wet Tropics bioregion of northeast Queensland is often promoted as the oldest continuous occurring primary rainforest on earth. Although global comparative scientific studies are lacking to substantiate this local lore, the antiquity of extant rainforest fragments and their strong Gondwanan relictual affinities is not disputed. It is widely accepted that the region contains patches of rainforest that are remnant or have served as arks for remnant lineages from Australia's mesic past millions of years ago prior to its separation from Antarctica and subsequent continental aridification. It is certain that this large-scale contraction of rainforest habitat was accompanied by periodic expansions and contractions coinciding with climate change, particularly during the glacial fluctuations of the Quaternary period (Hilbert et. al 2007). An accumulating body of molecular evidence (Crisp et al. 2010; Richardson et. al. 2011) strongly suggests that amidst these dynamic changes, the refugial elements of the contracted rainforest flora were also competing with an influx of species well adapted to tropical moist conditions from Southeast Asia as the Australian and Sundanian plates collided, shortening the distance required for intercontinental dispersal. The massive orogeny event (ca. 5 mya) that uplifted the northern portion of New Guinea, creating the New Guinea highlands is also likely to have facilitated long distance dispersal and floristic interchange of more temperate or high elevation adapted lineages.

This complex and ancient history would have undoubtedly left a signature in the extant distributions of flora and fauna in the region. The last two decades have witnessed major advances in the capacity and availability of molecular tools to measure and visualize evolutionary history in extant species assemblages. This has varied from the ability to trace the history and genetic diversity of one species through phylogeographic methods (Avies 2000) to the identification of larger scale patterns using phylogenetic diversity (PD) indices (Faith 1992). The Queensland Wet Tropics are often regarded as one of the most intensively studied tropical regions on the earth and are considered ideal for demonstrating new innovative methods that can then be applied in other under-studied regions (Moritz et al. 2005). Phylogenetic diversity and genetic diversity studies have been conducted in the region intensively for many faunal groups.

Endemic vertebrates in northeast Queensland are mostly confined to cooler rainforest above 300 m (Schneider & Williams 2005), which forms part of a larger “mesotherm archipelago” that stretches from New South Wales to New Guinea in a series of semi-isolated islands separated by lower and warmer regions (Nix 1991). Analysis of mtDNA variation in mammals, birds, frogs and lizards across the QWT has revealed the impact of Pleistocene and older glaciation events on historical population dynamics (Joseph and Moritz 1993; Joseph et al. 1995; Moritz et al. 1997; Schneider et al. 1998; Schneider and Moritz 1999; Schneider et al. 1999). Many species of vertebrates do not occupy all suitable habitats suggesting that local extinctions have occurred as a result of climate driven contractions and expansions of rainforest. Similar studies were conducted for arthropods in the Wet Tropics showing that climatic fluctuations promoted genetic diversity through vicariance, but reduced local species diversity through local extinction (Bouchard et al. 2005). These studies form a basis for research on rainforest refugia or the occurrence of evolutionary hotspots across the landscape. Patterns of faunal diversity within the region were clearly affected by Quaternary fluctuations with the ebb and flow of rainforest refugia areas acting as both a species “filter” (Schneider & Williams 2005) and a “pump” (Haffer 1969) of genetic diversity within species.

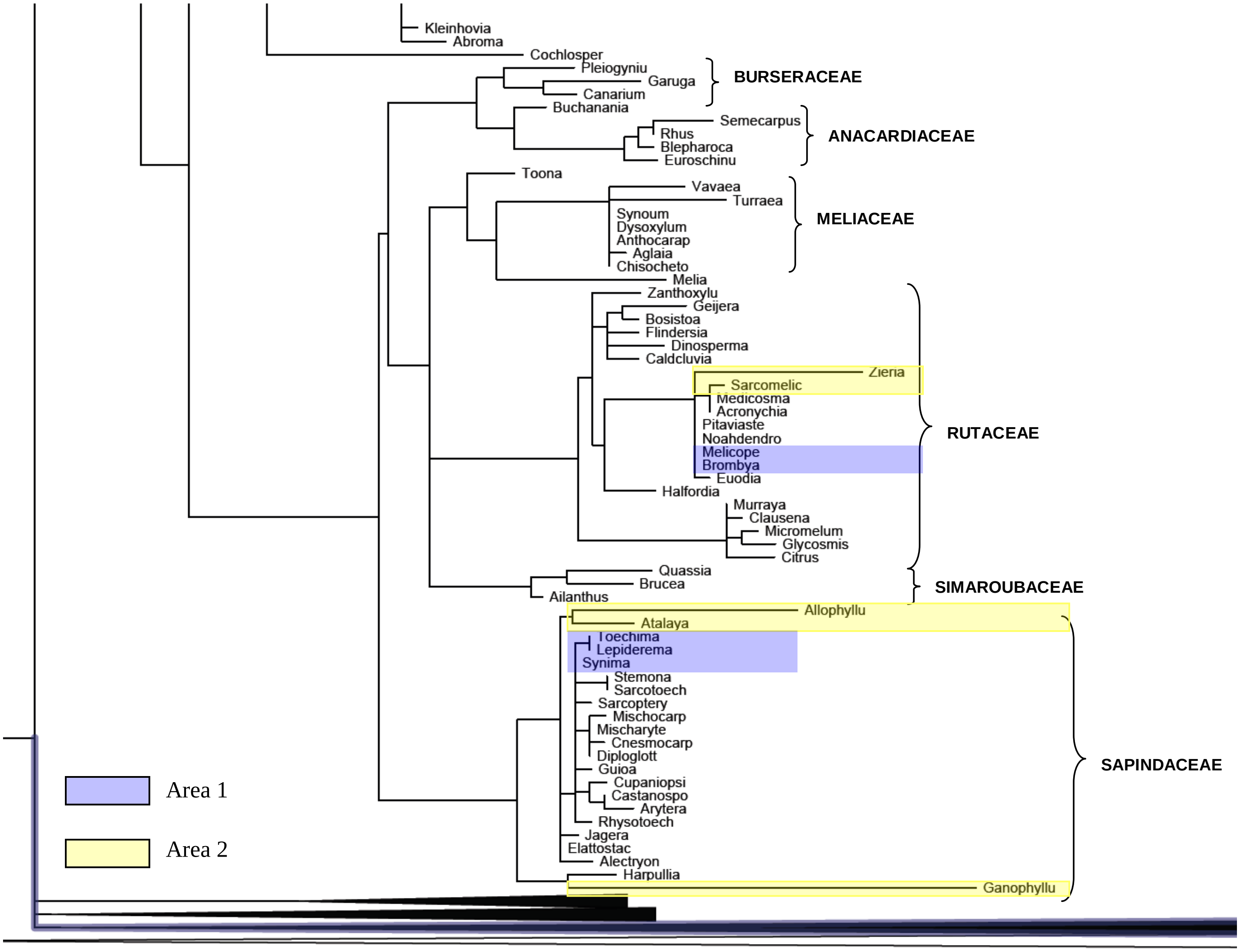
Although much work has been done on faunal groups in the region to date very little phylogenetic work has been conducted on the Queensland Wet Tropics flora. At the onset of this project the majority of the wet tropics flora had not been sequenced for DNA. This study aims to advance molecular knowledge of the region’s flora and assess large-scale patterns of evolutionary history across the landscape. To do this we have constructed a phylogeny of all angiosperm genera occurring in a network of 238 plots across the region. We then assess the phylogenetic diversity of this plot network and compare the results with diversity measures calculated from taxonomic richness data (e.g. number of genera and species). By assessing the correlation between these indices we assess both the robustness of the current taxonomy and its ability to predict PD and hotspots of evolutionary history. We then assess what other factors may help explain the observed patterns of PD, specifically the influence of foreign floristic elements co-existing with the extant Gondwanan flora, and the influence of elevation on community turnover.

PD theory initially suggests that quantifying the number of genera in a given area should not by default accurately reflect the relative phylogenetic diversity of that area. For example, using the topology of our tree from the order Sapindales (Figure 1); two hypothetical areas each have three Sapindaceae species and two Rutaceae species. The first area (blue) contains *Toechima, Lepiderema,* and *Synima* from Sapindaceae and *Melicope* and *Brombya* from Rutaceae while the second area (yellow) contains *Allophyllus, Atalaya,* and *Ganophyllum* from Sapindaceae and *Zieria* and *Sarcomelicope* from Rutaceae. Clearly Area 2 will have a higher PD value due to the branch lengths of the lineages present thus PD theory predicts that a direct correlation between taxonomic diversity and phylogenetic diversity is not expected. The prior or prerequisite to this logic must assume that that phylogenetic structure and community assembly of species at a given spatial scale is essentially random. Our null hypothesis is thus that there is no correlation between phylogenetic diversity (PD) and genus richness (GR). If this turns out to not be true then other environmental factors and variables may be considered for explaining variance in PD.

We assessed additional or other possible abiotic and biogeographic factors that may help to explain the distribution of PD through spatial and statistical analyses. Where are the hotspots of evolutionary history? Do they coincide with refugia areas predicted based on rainforest stability through time thereby highlighting the museum effect (Erwin 1991) or do we find more phylogenetic diversity in areas associated with more recent rainforest expansion or convergence zones suggesting the importance of the “cradle” (Mittermeier 1988; May 1990) for preserving evolutionary history? Has latitude or altitude influenced the distribution of PD or are the observed patterns more complex and consistent with other biogeographical sub-regions and/or boundaries? Given the substantial evidence in the historical and recent literature documenting an Indomalayan incursion of floristic elements present in the Queensland Wet Tropics flora, we expect that there should be some signature for this in the landscape on a spatial scale across the biome.

In a prelude to this study Richardson et al. (2011) reported that the incursion of Indomalayan (Sundanian) lineages into north Queensland was more successful in the lowland rainforests while uplands retained more Gondwanan or Australasian lineages. The explanation for this was hypothesized to be phylogenetic niche conservatism due to the dominance of lowland rainforest in Southeast Asia during the Miocene. If these inferences are true, we should expect to find some geographic pattern in the results of the present study that distinguishes the lowland and upland areas and/or areas with a higher proportion of Sundanian versus Gondwanan elements. Following this pretext, areas that contain a higher percentage of a foreign floristic element (in this case Sundanian) coinciding with the endemic flora (in this case Gondwanan) are hypothesized to have a higher phylogenetic diversity (PD) then expected based on genus richness (GR) because of the greater divergence between species of different floristic affinities.

Figure 1: Example comparing two areas with equal number of taxa with varying branch lengths.



METHODS

We utilized data from a plot network compiled and maintained by CSIRO Tropical Forest Research Centre in Atherton. The dataset is comprised of 238, 0.1 hectare plots which span the Wet Tropics bioregion of tropical northeast Queensland. These plots form the basis of vascular plant surveys for the region to: correct deficiencies in data collection (ie. gaps), assess specific rainforest types and to build up existing knowledge for distribution patterns of species, endemism, and diversity (Metcalfe and Ford unpublished data). All species present with these plots have been recorded in addition to some relative abundance, seedling, and biomass estimation data. Data utilized for the current study from this survey was presence/absence data of families, genera, species, elevation and GPS location. We sampled leaf tissue of at least one species for each genus occurring in the plot network. Samples were collected from either fresh leaf material, which was then desiccated and preserved in silica gel or from herbarium specimens ≤ 10 years of age. All fresh sampled individuals from the field were vouchered (Table S1) and deposited in the local herbarium (CNS).

Total genomic DNA was extracted using the Machery Nagel Plant II DNA Extraction Kit with the PL2/PL3 buffer at the Australian Genome Research Facility (AGRF, Adelaide Australia). Successful amplification of the official DNA barcoding locus *rbcLa* was attempted for each sample following the PCR protocol and procedures recommended by the CBOL Plant Working Group (2009). Samples that did not yield successful DNA or PCR product were replaced with sequences from GenBank (see below). The *rbcLa* locus (550 bp) was amplified using the primers and protocols specified by the plant DNA barcoding working group for the specific regions: *rbcLa* (ATGTCACCACAAACAGAGACTAAAGC) and *rbcL*a (GTAAAATCAAGTCCACCRCG). Thermal cycling parameters were two minutes at 95°C, 35 cycles of 30 seconds at 95°C, 30 seconds at 55°C, and one minute at 72°C, then final extension for two minutes at 72°C. PCR products were vacuum dried then purified and sequenced at the Australian Genome Research Facility (AGRF). A small percentage of DNA samples were sent to the Canadian Center for DNA Barcoding (CCDB), amplified and sequenced according to their protocols and submitted to the Barcode of Life Data Systems (BOLD) database for subsequent data release (Ratnasingham and Herbert 2007).

In total, 585 new sequences were generated representing 585 distinct genera spanning 43 orders and 129 families of flowering plants. Sequence data for a total of 71 genera was obtained directly from GenBank (http://www.ncbi.nlm.nih.gov/genbank/). This included many species which were identical to the species occurring in northeast Queensland. Where identical species could not be obtained and/or sourcing of fresh material and/or herbarium specimens for DNA extraction proved unsuccessful representative species from GenBank were selected for the respective genera based on their known geographic distributions. In all cases, the representative species were chosen based on their floristic proximity in taxonomy and natural distribution to the northeast Queensland tropics.

Consensus sequences were assembled using ChromasPro v.1.32 and DNA Baser Sequence Assembler v.3 (2011) then aligned with MAFFT online v. 6 (http://mafft.cbrc.jp/alignment/server/), then checked manually with BioEdit Sequence Alignment Editor v.7.0.9.0 (Hall 1999). The final alignment of *rbcLa* (600 base pairs) for 658 genera was analyzed using the maximum liklihood (ML) method in PHyML (Guindon et al. 2010) using the HKY85 substitution model with estimated gamma shape paramaters and optimised topology and branch lengths. Results were then imported into Biodiverse (Laffan et al. 2010) to calculate PD (Faith 1992), and the richness of species and genera were plotted against the results of PD per taxonomic unit at four different spatial scales.

To examine the ability of genus richness (GR) to predict phylogenetic diversity (PD), we tested the relationship between these two measures via regression at four spatial scales (grid cells with length and width dimensions of 0.1 hectares, 0.0625º, 0.125º, and 0.25º). Presence absence data from the 0.1 hectare spatial resolution was amalgamated into grid cells for the three higher spatial scales in Biodiverse. Although GR is expected to explain some component of PD (see Results), we were also interested in examining the extent to which spatial position within the landscape, may explain PD. The Queensland Wet Tropics is a biogeographical complex dynamic landscape with multiple layers of evolutionary history that have accumulated through time. Areas with different evolutionary histories may contain similar levels of GR but different levels of PD. To investigate this we plotted the residual values from previous analyses in space and examined geographic distribution of locations with more (positive residuals) or less (negative residuals) PD than is expected based on GR. The residuals are a measure of what GR cannot explain thus plotting them in geographical space tests for other factors that may influence PD by identifying any patterns that may exist at particular spacial scales. We separated the residuals into 6 classes (see Results), color coded proportional to their relative positive and negative values (yellow = negative residual, blue = positive residual).The spatial analyses were performed and mapped using Biodiverse and DIVA-GIS v.5.2 (Hijmans et al. 2005).

Because our data come from geographically explicit locations both PD and GR are likely to show significant spatial autocorrelation. This can be a potentially large problem in datasets such as ours because it reduces the independence among model residuals, inflating the type I error rate (Legrende et al. 2002, Huang et al. 2011). We first examine spatial autocorrelation in PD via Moran's I correlogram. We then used spatial eigenvector mapping (SEVM), generated through Principal Coordinates Neighbour Matrices (PCNM) to explicitly account for this influence (Diniz-Filho and Bini, 2005). Geographic location information was based on decimal latitude and longitude of the center of each grid cell and a truncation distance (calculated in SAM-Spatial Analysis in Macroecology (Rangel et al. 2010)) of 0.428 decimal units was used to create spatial filters. Three eigenvector filters were then chosen based on their influence on PD being both statistically significant ($P < 0.05$) and having sufficient explanatory power ($r^2 < 0.02$) (after Huang et al. 2011). Competing regression models were then generated based on all possible combinations GR and the three spatial filters, which were then compared for their ability to describe PD. Sample size corrected Akaike information criterion (AICc) was used to evaluate the goodness of all model fits. The model with the lowest

AICc score was considered to be most informative given the number of parameters used in model formulation (Burnham and Anderson, 1998) although all models having ΔAICc values ≤ 2 were considers as having substantial support as approximating models. To visualize the geographic distribution of the component of PD that could not be described by either GR or any spatial filter, we then mapped the residuals from the best approximating model on locality point data for our sample sites.

Plotting residuals (see above) indicated further possible structuring unaccounted for by either GR or spatial filters (see results). Richardson et. al (2011) hypothesized that within the wet tropics, altitude is a good predictor of the ratio of plant species that are derived from Gondwanan lineages and those derived from the Indomalayan region. Such bias in ancestry could influence PD, which would tend to be higher in sites that contained species of most divergent ancestry. To assess this possibility, we included two further predictor variables (altitude (alt) and the proportion of species within each local community that were known to be from Gondwanan lineages (p(Gond)) in another round of model fitting with spatial filters identical to that described above. Again, model selection was based on AICc. We also checked for the ability of inclusion of spatial filters to remove possible influence of spatial autocorrelation by plotting residuals from the best approximating model via Moran’s I correlogram (Diniz-Fihlo et al. 2003).

Floristic origins data from Richarson et al. (2011) was utilized to assigns three categories of floristic origin to all genera present; 1.) Sundanian, plants which have dispersed southeast from the Sunda plate, 2) Australasian, plants which originated in the Gondwanan land mass and persisted in Australia or dispersed northwest, and 3) Unresolved lineages of plants for which data is lacking to assign a floristic origin. This dataset was linked to our 0.1 hectare plot data then richness of Australasian and Sundanian taxa was calculated in Biodiverse. Percent of each floristic element was then calculated by dividing these numbers by the total number of species in each plot.

RESULTS

Tree Topology

The maximum likelihood analysis produced a tree that is similar in topology to the APG III tree (Angiosperm Phylogeny Group 2009). Figure 2 shows the entire tree labeled to order and major APG subgroups. Subtrees for each of the APG subgroups (Supporting Information, Figures S1-S9) are labeled to family and genus level. Below is a brief review of the topology of these subtrees to identify any inconsistencies with the APG III tree that may have resulted from the many new genera we now have sequence data for as a result of this project and to highlight any new information or inferences to be made from this that may be worthy of further investigation following this project. We utilize the old sub-classification names Eurosids I & II and Euasterids I & II, which are now recognized in APG III in same order as above as the Fabids, Malvids, Lamiids, and Campanulids.

The basal angiosperm subtree (Figure S1) is mostly consistent with the APG topology with the exception of the placement of Hernandiaceae, which should be nested within Laurales, and Austrobaileaceae, which should be basal to all other families. This is likely due to the fewer characters represented in our dataset of only the *rbcLa* barcoding region. Also, an additional tree was generated (not shown here) simply by pruning the gymnosperms then re-rooting the tree on Austrobaileaceae. The topology then more accurately reflected the APG topology. Other points of interest in this subtree is the exceptionally low rate of variation in Monimiaceae, a classic Gondwanan family, and Lauraceae. All genera in Monimiaceae have very little variation with the exception of *Palmeria*. The order Piperales shows high variation between genera and the family Annonaceae contains both long branched groups and short branch groups as documented on a global scale previously without all the Australian genera (Richardson et al. 2004).

The only major discrepancy in the monocot subtree (Figure S2) from APG III is that Zingiberaceae is not sister to the Commelinoid clade. The placement of the remaining families is more or less consistent with APG III. Of interest is the Commelinoid clade, which stands out as a whole with the deepest divergence from the rest of the monocots having the longest crown and stem nodes for each family. The family Aracaeae also shows two interesting distinct subgroups, one with no variation at the genus level in our tree and a second clade with deep diverging branches. A few scattered long branched taxa occur nested within shorter branched clades including the widespread Indomalayan and Pacific *Scleria brownii* (Cyperaceae), *Aphyllorchis* represented by the Southeast Asian *A. caudata*, and *Apostasia stylidioides* (Orchidaceae).

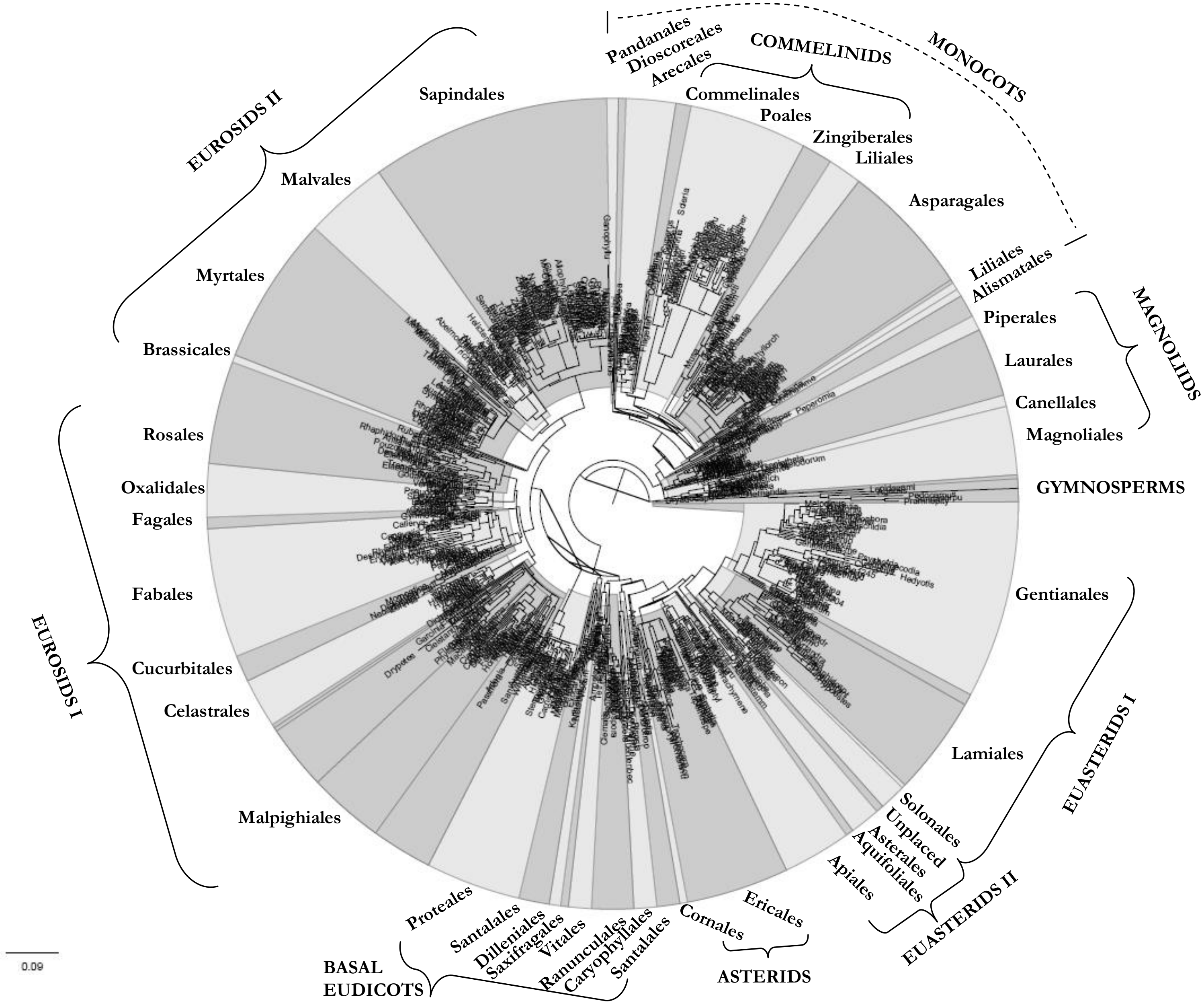
The topology of the basal and core eudicot subtree (Figure S3) is not well resolved. Santalales is shown to not be monophyletic with Loranthaceae grouped with Caryophyllales and Polygonales instead of Santalales while Dilleniaceae is grouped with the remaining Santalales. In addition two basal Rosid families Vitaceae and Hamamelidaceae are grouped with Ranunculales. This is likely because most of the basal eudicot families are absent from our tree, which only contains Proteaceae and Ranunculales. All families and genera are well distinguished however making the tree sufficient for the purposes of the present study. Of particular interest in this subtree are the two basal genera in Proteaceae: *Eidothea* and *Placospermum*. *Eidothea* contains only two species in the entire genus, both are restricted in distribution with one in the upland rainforests of Northeast Queensland and the other listed as Endangered in New South Wales. *Placospermum* is also a relict lineage being a monotypic genus endemic to Northeast Queensland but it is more common in distribution as it favors disturbance.

The Eurosids, formerly referred to as Eurosids I & II, were renamed the Fabids and Malvids in the APG III tree. Our Eurosids I (Fabids) subtree (Figure S4) shows genera with noticeably longer branch lengths then the previous two subtrees. The topology of this tree is not exactly the same as APG III however all orders and families are accurately distinguished. The new circumscription of the former Euphorbiaceae sensu lato is well illustrated in Figure S5. The former Euphorbiaceae genera now placed in Picrodendraceae are shown to be paraphyletic with Euphorbiaceae sensu stricto separated by several distinct families while the new families Phyllanthaceae and Putranjavaceae are both nested within a clade separate from Euphorbiaceae sensu stricto. Of interest in the Eurosids I is the genus *Storckiella* (Fabaceae), which comes out as basal to all other Caesalpinioidea and Faboidea. Our preliminary data suggests this is an early diverging member of the Fabaceae family and its restricted distribution would indicate it is a relict lineage that either has not undergone much speciation or that it has and subsequently undergone extinctions leaving only one extant species in Australia. This is in direct contrast to another clade within Fabaceae, subfamily Mimosoideae, which shows several genera with very little variation between them. Each of the genera in this Mimosoideae clade all have numerous species, many of them are local endemics thus Fabaceae shows patterns of having both recently radiated and relict lineages.

A similar pattern is found within Myrtaceae in the Eurosids II (Malvids) subtree (Figure S6), which shows numerous genera with little variation and a few scattered genera with notable longer branch lengths. The same pattern is even more evident in the order Sapindales in Eurosids II (Figure S7) with each family represented almost entirely by genera with short branch lengths except for one or two genera with comparatively very long branches. The placement of Myrtales was uncertain in earlier versions of the APG tree, which could not confidently place it in either Eurosids I or Eurosids II. Our tree is consistent with APG III placing Myrtales within the Eurodids II (Malvids) and both Eurosid groups are correctly circumscribed.

The Euasterids I & II were renamed the Lamiids and Campanulids in the APG III tree. Both subgroups are correctly distinguished in our tree. Within our Euasterids I (Lamiids) subtree (Figure S8) the former family Asclepiadaceae is visible nested within Apocynaceae, which necessitated the synonymy of the former family. Rubiaceae, one of the most diverse families in our dataset is shown to contain many very closely related genera. A few of the genera that show greater divergence with long branches are mostly widespread, pantropical taxa. Of interest in our Euasterids II (Campanulids) subtree (Figure S9) are a few families that have been traditionally poorly understood, several of which were previously lumped into Icacinaceae, a classic garbage can family. There is only one surviving member in our dataset of the traditional family Icacinaceae, which remains an unplaced family. *Apodytes* (Icacinaceae) is placed at the base of the tree next to Cornaceae. The genus *Sphenostemon* has been previously placed in Aquifoliaceae and Sphenostemonaceae and now sits within Paracryphiaceae, which is supported by our tree. *Pennantia* was previously treated under Icacinaceae but now is recognized as a monotypic family within Apiales. Our tree however places it between Paracryphiales and Escalloniales. Other groups are not resolved in our tree including Apiales, in which the two families Apiaceae and Araliaceae do not come out as monophyletic. The order Aquifoliales also does not come out monophyletic with Stemonuraceae nested within Asterales.

Figure 2: ML tree for all genera present in plot network.



Patterns of observed PD

Visual comparison of spatial mapping of PD verses the richness of genera (GR) (Figures 3) suggests a very strong correlation between the two indices. Two hotspots of PD are clearly identified (Figure 3a). A large southern hotspot located on the Atherton Tablelands and the southern Cairns-Cardwell lowlands (hotspot 1) and a smaller northern hotspot in Cape Tribulation (hotspot 2) located north of the Daintree River. These two areas are more clearly identified when a larger grid cell size is utilized (Figure 4a) at 0.625°. For example, low PD is observed between the northern and southern hotspots of which a large percentage is occupied by the area known as the Black Mountain Corridor (BMC). The BMC in Figure 3 shows some scattered cells with moderate levels of PD, which are not evident when samples are combined in larger grid square (Figure 4) indicating it to be an artifact of sampling size. All rainforest sections in the BMC, south of hotspot 1, and west and north of hotspot 2 are notable in having consistently low levels of PD. Very little visual discrepancy is evident between GR and PD on a spatial scale suggesting that GR is an accurate predictor of PD in the Wet Tropics bioregion. Visual inspection of the same data where PD is plotted against GR in graph form (Figure 5) strengthens this inference.

A strong and significant positive relationship between GR and PD at all spatial scales was evident at initial inspection of the data (Figure 5). Nevertheless, there was significant spatial autocorrelation associated with PD among sites (solid symbols on Figure 6). In the first round of analyses, GR was identified as a significant explanatory variable in determining PD (Table 1), although in all cases the best approximating model included (at least) one spatial filter (Table 1). At the 0.1 ha scale, comparisons based on AICc, however, identified just one of the possible 14 competing models as the most informative approximation (no alternative models had ΔAICc values ≤ 2). A single best-approximating model was also identified for 0.25° grid squares, but for the other two scales, one or more models had ΔAICc values <2 (i.e. at 0.0625° there were two well supported models, while at 0.125° there were four). In all cases, the best fitting model included GR, and, as expected, its influence was positive (Table 1). Coefficients for GR in models were 0.05 at 0.1ha scale, but slightly lower for scales amalgamating sites (0.033, 0.032, 0.028 for 0.0625º, 0.125º and 0.25º grid cells respectively) (Table 1). Furthermore, in all cases R^2_{adj} values were high indicating that a high proportion of the variation in PD could be explained by GR and spatial filters alone (87.5% (0.1ha); 91.9% (0.065º); 97.3% (0.125º); 97.6% (0.25º).

Figure 3: Phylogenetic diversity (a) and richness of genera (b) at 0.1° grid cell resolution

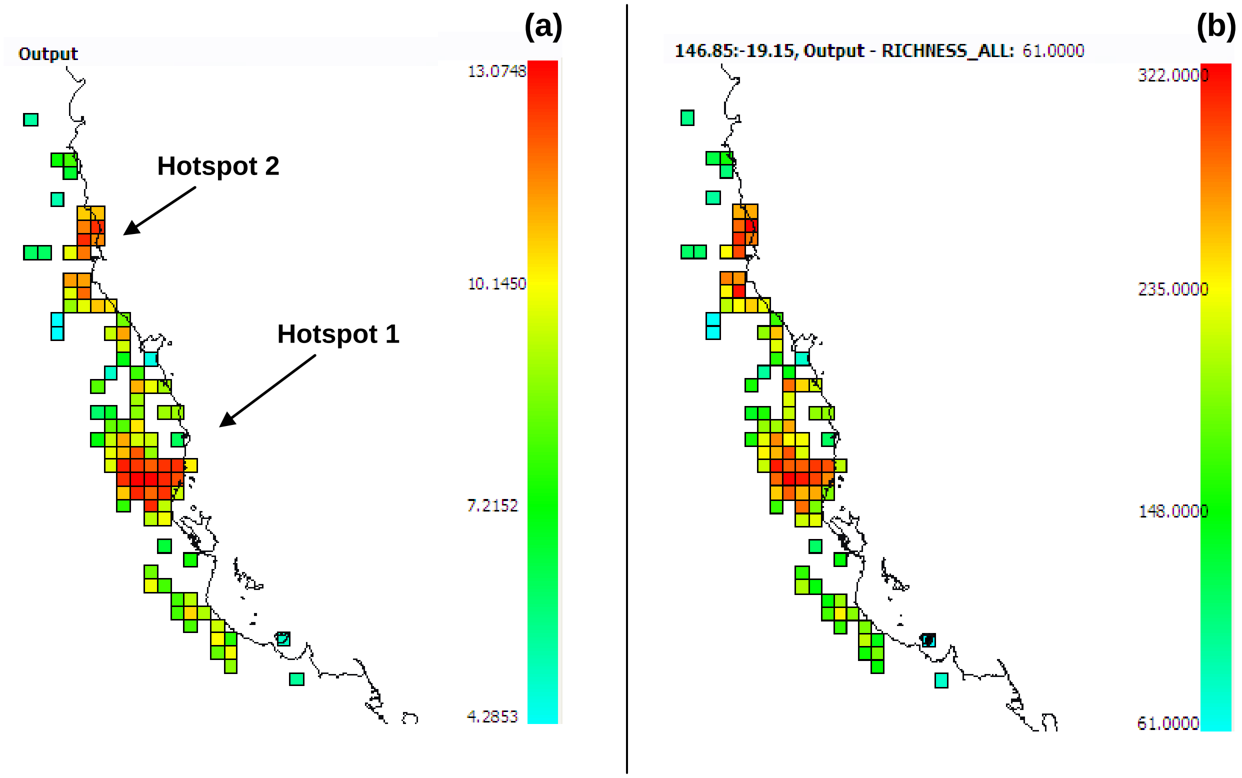


Figure 4: Phylogenetic diversity (a) and richness of genera (b) indicated by color coded scale bar at 0.0625° grid cell resolution.

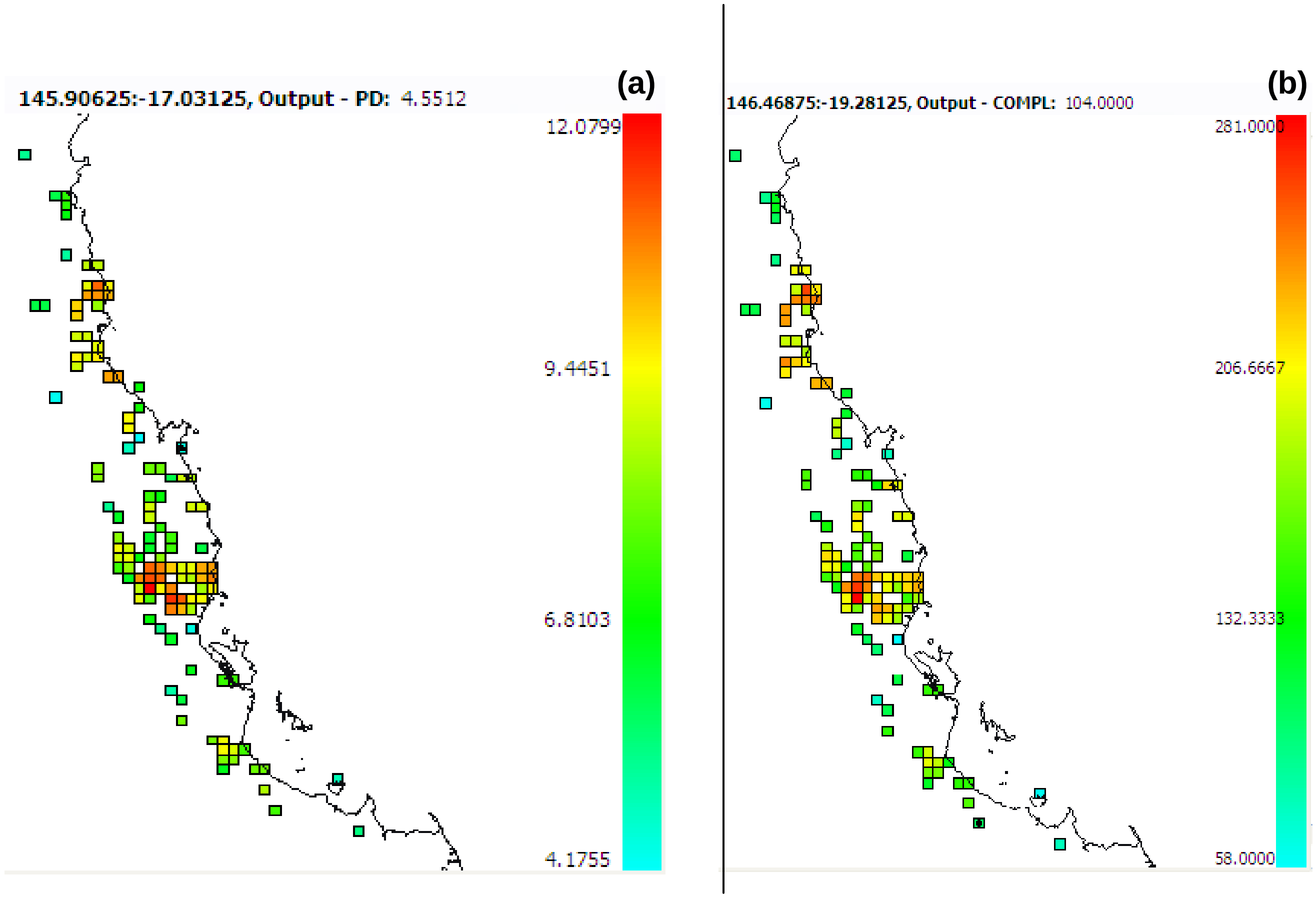


Figure 5: The relationship between PD and GR at four different spatial resolutions; 0.01 hectares (black), 0.065º (red), 0.125º (green) and 0.25º (blue).

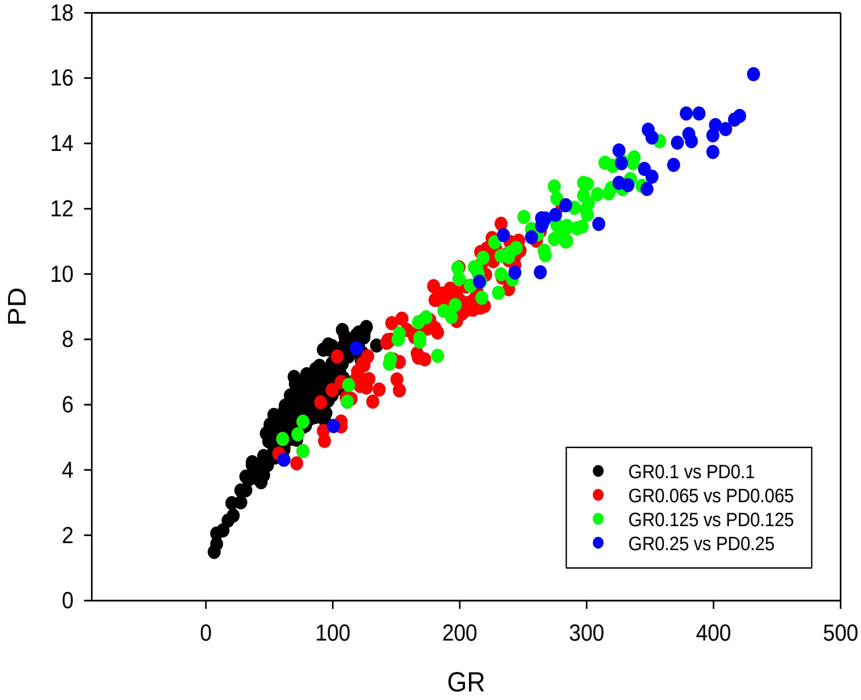
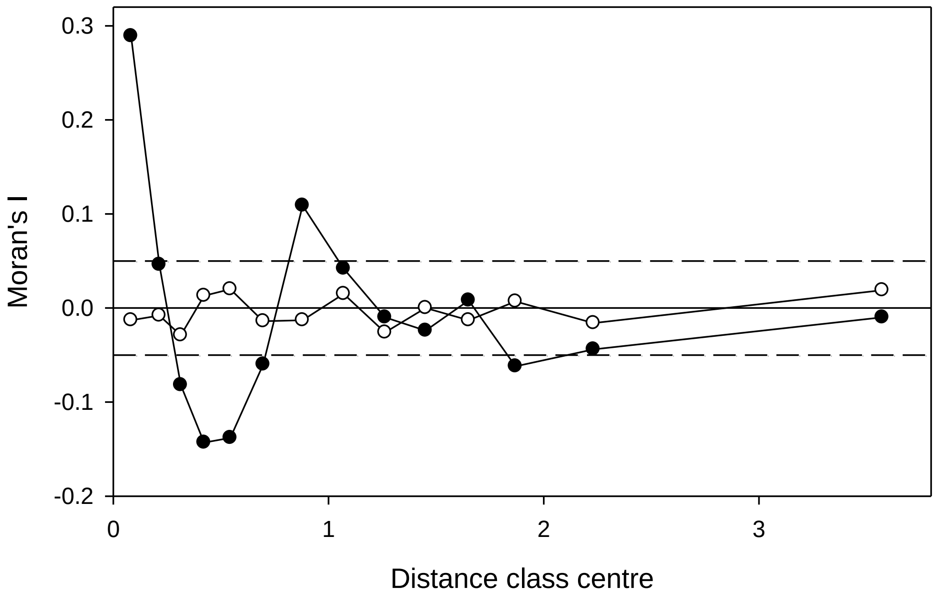


Table 1. Standardised regression co-efficients (*b*), *t* statistics, and associated *P*-values of the best fit multiple regression model to explain PD based on a single predictor (GR = generic richness) and three spatial filtering variable conducted at four different spatial resolutions. The single model presented for each spatial resolution was that with the lowest AICc value.

Variable	*b*	t	*P*
Scale 0.1 ha			
Constant	1.943	18.788	<0.001
GR	0.05	39.673	<0.001
SF3	1.92	4.087	<0.001
Scale 0.0625^o			
Constant	2.675	15.99	<0.001
GR	0.033	34.789	<0.001
SF2	2.466	4.735	<0.001
Scale 0.125^o			
Constant	2.78	15.299	<0.001
GR	0.032	42.243	<0.001
SF1	-0.799	-1.832	0.071
SF2	1.848	4.691	<0.001
SF3	-2.303	-5.161	<0.001
Scale 0.250^o			
Constant	3.6	13.707	<0.001
GR	0.028	34.225	<0.001
SF1	-1.528	-3.297	0.002
SF2	2.718	6.398	<0.001

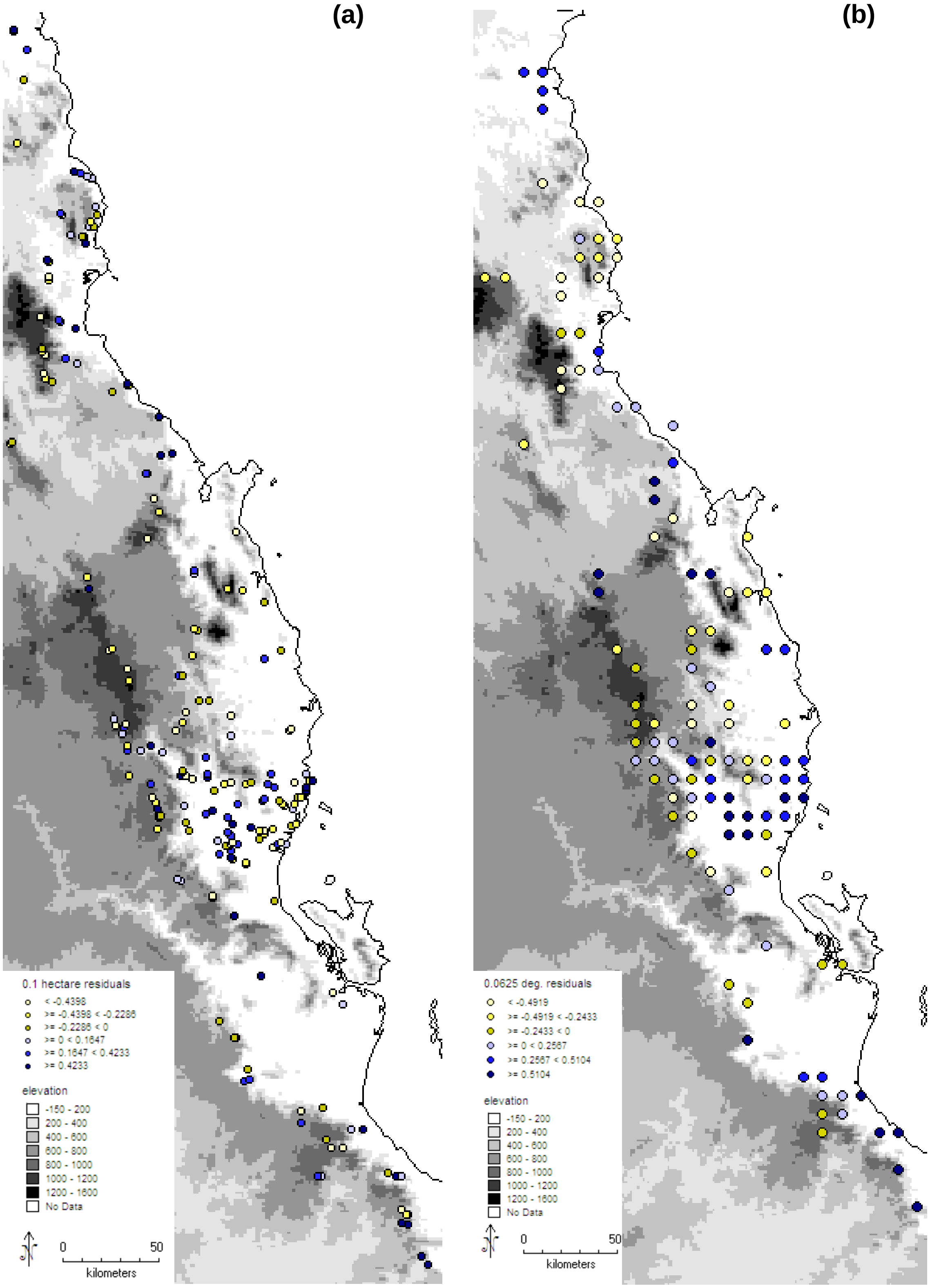
Figure 6: Moran's I correlogram for PD (solid symbols) and the residuals of multiple regression with predictors and spatial filters for best fitting model (open symbols) for plant species community composition in xx 1ha sites in wet tropics region of north Queensland, Australia.



Nevertheless, when the residual (unexplained) variation from the regression models were mapped back onto the spatial locations associated with study sites, there appeared possible further structuring associated with elevation (Figure 7). Positive residuals are found in areas with both high and low PD and vice versa for the negative residuals however there does appear to be a pattern associated with elevation. Few positive residuals are found in the upland sites. Negative residuals are found in both the uplands and lowlands but appear more biased to the uplands. A pattern is more evident at the 0.0625º scale.

At the 0.0625º scale, (Figure 7b) positive residuals (blue) are clustered in the southern hotpot in the Cairns-Cardwell lowlands, in the Black Mountain Corridor, and in the northern most area at the WT bioregion boundary. Few negative residuals (yellow) occur in the lowlands. The majority are found in the northern Daintree hostpot area, and the Atherton, Carbine, and Windsor Tablelands where few positive residuals occur. The pattern becomes less clear at the next two higher spatial scales as the data becomes further amalgamated (Figure S10).

Figure 7: Negative residuals (yellow) and positive residuals (blue) at 0.1 hectare scale (a) and 0.0625° scale (b).



In the second round of model fitting conducted for 0.1ha resolution which included the two new terms altitude and proportion of Gondwanan taxa, three spatial filters were again identified as potentially important. Of the 61 candidate models, four were considered to have substantial support as approximations for PD (Table 2). As in the initial analysis, all four models included both GR and SF3. All four models also included one of the the new predictor variables p(Gond). The most informative model contained these three factors only, while the other three models included these plus either SF2 (model 2), SF1 (model 3) or $\log_{10}$Alt (model 4) (Table 2). Based on Akaike weights (Wi) we selected model 1 for more detailed analysis.

The final model showed significant positive association between PD and GR, and PD and SF3. However, in support of the hypothesis that increased proportion of species within local assemblages from lineages that are not Gondwanan was associated with higher PD values, the standardised co-efficient for p(Gond) was negative (Table 3) . This model was a significant improvement over the original ($R^2_{adj} = 0.908$) and the ΔAICc value for the original model with the inclusion of the new terms was 71.73. Further, the spatial correlogram based on Moran's I index suggested that the inclusion of the single spatial filter was sufficient to overcome pattern of spatial autocorrelation in the residuals of the regression (open symbols on Figure 1).

While we found that the best approximating model did not include both Log_{10}Alt and p(gond), one model with substantial support did include both variables (model 4) (Table 2). At this point it is uncertain whether including both terms is important. Spatial correlation between p(Gond) and Log_{10}Alt was significant and positive (n = 236, Pearson's r = 0.452, $F_{corrected} = 58.607$, $df_{corrected} = 227.773$, P <.001), suggesting that the proportion of species in a local assemblage that are from Gondwana lineages increases with increasing altitude in these forests. In that respect, the component of the total variation in PD explained by these variables may overlap.

Table 2: Summary of model selection. The four models representing equally valid descriptions of the distribution of PD. ΔAICc values were compared to the best fitting model. Wi is the Akaike weight indicating the relative support for a given model when compared with other models. K is the number of variables, including intercept. Predictor variables are; GR = generic richness, p(Gond) = proportion of species in community sample known to be derived from Gondwanan lineages (see text for details), logAlt = log10 altitude of 1Ha study site. Spatial filtering variables determined via (PCNM) SF1 – SF3.

Model	Adjusted R^2	AICc	ΔAICc	K	Wi
GR, p(Gond), SF3	0.908	227.114	0	4	0.304
GR, p(Gond), SF2, SF3	0.908	228.679	1.565	5	0.139
GR, p(Gond), SF1, SF3	0.908	228.785	1.67	5	0.132
GR, p(Gond), logAlt, SF3	0.908	229.065	1.951	5	0.115

Table 3: Standardised regression co-efficients (*b*), *t* statistics, and associated *P*-values of the best fit multiple regression model identified in Table 1. GR = generic richness, p(Gond) = proportion of species in community sample known to be derived from Gondwanan lineages (see text for details), SF3 spatial filtering variable determined via (PCNM).

Variable	*b*	t	*P*
Constant	3.084	19.913	<0.01
GR	0.05	46.135	<0.01
p(Gond)	-1.873	-9.012	<0.01
SF3	1.032	2.473	<0.01

DISCUSSION

Patterns of tree topology and observed PD

Visual inspection of our tree topology shows a wide range of branch lengths across taxa. Some families such as Lauraceae (Figure S1) and Sapotaceae (Figure S9) are represented nearly entirely by genera of short branch lengths, some with all long branch lengths such as Ericaceae (Figure S9) and Apocynaceae (Figure S8), and others with a combination of both including Myrtaceae (Figure S6) and Fabaceae (Figure S4). The rate of nucleotide variation between families and even within families varies substantially throughout the Angiosperms. This may be attributed simply to natural variation in mutation rates between lineages. In some cases however, the variation may indicate that the Wet Tropics bioregion contains a diverse array of lineages of different evolutionary histories including groups that have recently radiated, relict lineages that may have undergone little change through time or are the sole remaining member of their lineage, and others that are divergent due their arrival in Australia from other continents in the last few million years.

A well supported example of a relict lineage is the basal Proteaceae genus in our tree, *Eidothea* (Figure S3), of which fossil evidence suggests that the two extant taxa are relict descendants from the same or similar species with a former more widespread distribution (Weston and Kooyman 2002a,b). This evidence supports the relict and refugial character of Australia's rainforest that is now restricted in distribution and home to groups that may the sole surviving member of their lineage. Simultaneous evidence occurs in our phylogeny of recent diversification. The basal angiosperms in particular (Figure S1), often referred to as "primitive," have an exceptionally low nucleotide substitution rate between closely related species re-emphasizing that many "ancient" lineages have undergone recent radiation and are thus only relict in terms of their ancestry. In other cases the variation among branch lengths within clades is explained by differing floristic origins. This undoubtedly occurs not only among different genera within families but has also been shown to occur within species of the same genus. The genus *Diospyros* was shown to have at least two separate lineages, one long branched clade and one short-branched clade, represented in Australia that dispersed at different time periods (Duangjai 2009). Costion et al. (unpublished data) extended this work to show there are actually three separate lineages of *Diospyros* with separate evolutionary histories all occurring simultaneously within the Wet Tropics.

Though data is lacking to reconstruct the detailed evolutionary history of the Wet Tropics flora here we show that broad scale patterns can be identified and visualized spatially using phylogenetic diversity and spatial autocorrelation analyses. Two hotpots of PD and GR are identified in this study that are consistent with previous work done in the region. Crisp et. al (2001) demonstrated that the Wet Tropics are the second most important centre of plant endemism in Australia and further defined two identical centers of endemism within the region, the Atherton Tablelands and the Daintree area. Hilbert et al. (2007) also inferred two primary rainforest refugia areas that were present during the last glacial maximum with similar boundaries to PD hotpots 1 and 2. The correlation between hotspots of PD and hotspots of taxonomic richness (GR) are statistically significant and would support the notion that these areas are evidence long-term refugia that have been more resilient to extinction through time.

Although a linear relationship between PD and GR has been previously reported at a bioregional scale (Forest et al. 2009), simply mapping alpha diversity does not capture the complexity of the evolutionary history of the region. Plotting the linear regression residuals enabled assessment for any finer scale patterns in the landscape that are hidden when viewing a direct comparison of PD and GR. A hidden pattern was unveiled that substantiates inferences on the presence of Indomalayan or Sundanian elements in the lowlands. Richardson et al. (2011) hypothesized that the establishment of lineages that dispersed from Southeast Asia (Sundanian element) into Queensland was biased to the lowlands primarily due to phylogenetic niche conservatism. Although the causes of this trend are not assessed here, the pattern is determined to be statistically significant. Areas that have higher PD than expected based on GR are positively correlated with areas that have a high percentage of Sundanian lineages, which are also correlated with low elevation.

Floristic Origin Data

The differences between Figures 7a and 7b may be accounted for by floristic origin data (Figures 8-9). When the 0.1 hectare plot data is amalgamated into 0.0625° grid cells site specific elevation data is lost. Figure 7b suggests that very few negative residuals occur in the lowlands however this is not consistent with evidence in the Cairns-Cardwell lowlands (Figure 7a). When the percent Sundanian and percent Gondwanan species present per site were plotted against elevation it is apparent that the Sundanian component is more influenced by elevation then the Gondwanan component. Percent Sundanian species decreases with an increase in elevation (Figure 8) however percent Gondwanan species (Figure 9) is not as strongly correlated with elevation. If the residuals from the PD/GR regression can be partially explained by percent floristic origin data then Figure 7a is consistent with the trend observed in Figures 8-9. Sites that are rich in Gondwanan elements are present in both the uplands and lowlands however sites that are rich in Sundanian elements are more restricted to the lowlands. Initial inspection of this data supports the inclusion of floristic origin data in a more complex explanatory model test.

Figure 8: Percent Sundanian species per site plotted against elevation

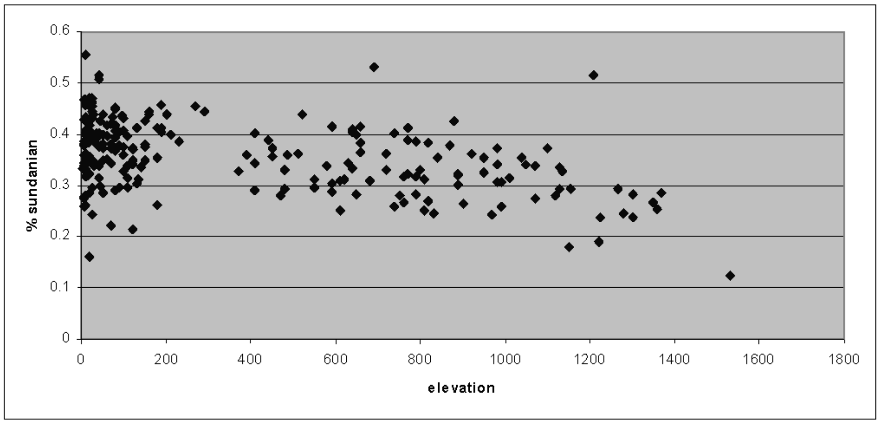
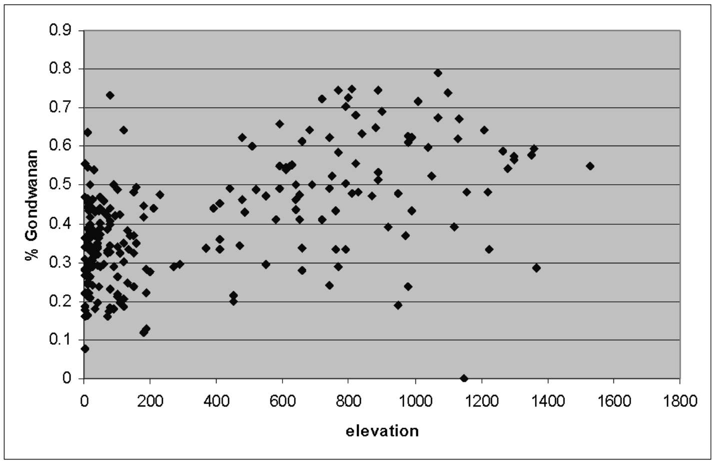


Figure 9: Percent Gondwanan species per site plotted against elevation



Patterns of phylogenetic diversity as evidence for biome assembly

The fossil record

A wealth of macro and micro fossil data exists in Australia that supports a widespread cooler rainforest flora for much of its history. Classic Australasian rainforest taxa recorded from Australia as early as the Cretaceous include Proteaceae, Podocarpaceae, Winteraceae, and *Nothofagus* (Dettnann 1994). Macro fossils from southeastern Australia indicate a diverse rainforest flora present during the Eocene dominant with Lauraceae and associated with Elaeocarpaceae, Cunoniaceae, many Proteaceae and Myrtaceae species, *Brachychiton* (Sterculiaceae), and Causarinaceae (Greenwood & Christophel 2005). These forests went through warmer (more tropical) and cooler (more temperate) phases but persisted until Australia's final separation from Antarctica brought about the formation of the Antarctic circumpolar current. This lead to a massive retraction of rain forest evident from Neogene microfloral and faunal data (Greenwood & Christophel 2005) which corresponded with aridification, cooler temperatures, northward drift of the continent, and increase in latitudinal temperature gradient. Rainforest progressively declined on a continental scale but persisted in small refugia along the eastern coast.

From the largest of these refugia in northeast Queensland, a prevalence of *Nothofagus* and Podocarpaceae fossils indicate a cooler more temperate climate than today for much of the Miocene. *Nothofagus* maintained a significant and stable presence up until the early Pliocene which corresponded with a temperature rise and increase in Asteraceae and Chenopodiaceae pollen (Kershaw 1988; Kershaw et al 2005). This would indicate a more temperate origin of its extant rainforests however the extant lowland flora of the region has also been considered the closest analogue to numerous macrofossil sites of southeastern Australia (Christophel 1981; 1994).

A megathermal flora similar to the modern tropical flora has been inferred from these sites for much of the tertiary in the lowlands of southeastern Australia. Direct support for connectivity between the southeast and northeast through time is lacking though the lack of latitudinal temperature gradient prior to widespread cooling lends support to this idea. Additional support has come from the early presence of *Nypa* and *Anacolosa* pollen in southern sites (Adam 1992) and the similarity of Early Miocene palynosequences from Southern Queensland and southeastern Australia (Macphail et al 1994). Both *Nypa* and *Anacolosa* are characteristic of tropical lowlands and today only occur in northeastern Australia. Today northeast Queensland maintains a diverse assemblage of vegetation types, many of which bare much similarity to fossil floras of different eras of Australia's history (Kershaw et al 2005). This attests to its refugial character and has attributed to its World Heritage status. Both upland sites rich in cooler temperate affinities and lowland sites in the bioregion have been inferred as long-term refugia (Webb & Tracey 1981; Hilbert et al 2007).

Although the Gondwanan heritage of this region is well accepted the influence of Sundanian or "Indomalayan "intrusive" elements present has remained contentious. Truswell et al (1987) indicated that there was fossil evidence for long distance dispersals from SE Asia to Australia during its isolation phase in the Tertiary and the Miocene but no evidence to suggest that this invasion was evidently massive or enhanced by increasing proximity of the Australasian and Sunda plates. This conclusion is now being turned on its head in light of a rapidly expanding body of molecular literature and the limitations of palaeobotanical data.

Continuous pollen sequences from northeast Queensland and Southeast Asia are sparse in comparison to southeastern Australia. There are no reliable dated tertiary sequences older than the late Oligocene from all of Queensland (Macphail et al 1994). More importantly pollen cores in the tropical north have been limited to the uplands (Kershaw 1988) and offshore marine deposits (Kershaw et al 2005). There are no lowland sites in the extant Queensland Wet Tropics to our knowledge, which as we shall discuss is crucial to understanding the Sundanian component. Kershaw (1988) noted both these limitations as significant and suggested the lowlands were the most likely place where interchange would be recorded. Further more, both Kershaw et al (1993) and Truswell et al (1987) indicated that the invading lineages would have most likely been insect pollinated taxa and thus difficult to detect in palynosequences. The “lack of support” for a strong Sundanian element in Australia’s fossil record is most likely biased by site locations, the sheer lack of fossil sites in the tropical north, and by the pollen dispersal and preservation capabilities of the fossilized taxa.

Affinities of the extant flora

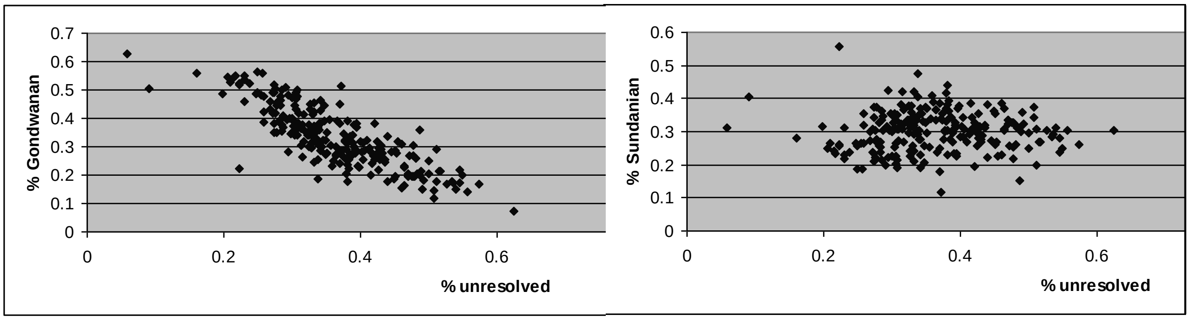
The Sundanian element is strongly supported by molecular data for numerous lineages (Richardson et al. 2011; Sniderman & Jorden et al. 2011; Crayn et al. in prep), of which few have had a strong presence in Australia’s fossil record. By stark contrast, all of the lineages designated as Gondwanan in this study (Richardson et al. 2011) are characteristic of Australia’s fossil floras (Hill 1994). Additional support for this notion is found in the present dataset by calculating the proportion of unresolved species compared to percent Sundanian and Gondwanan species.

It is expected that a higher proportion of the unresolved taxa are not Gondwanan due to many of these being widespread pantropical taxa or Genera that are very species rich in Southeast Asia (Richardson et al. 2011). Since lineages that have recently dispersed then adapted to the Queensland Wet Tropics are less likely to have left fossil evidence there should be a higher proportion of unresolved taxa that are of Sundanian or other foreign origin. Direct support for this hypothesis was observed (Figure 10).

A proportion of taxa cannot be resolved with current available data to a particular floristic origin. The percent unresolved taxa were calculated then p(Gond) and p(Sundanian) per site is plotted against p(unresolved species) per site to assess if unresolved taxa were more likely to fall within one or the other categories (Figure 10). There was no significant spatial correlation between p(sund) and p(unresolved) (n = 236, Pearson’s r = 0.018, $F_{corrected}$ = 0.066, $df_{corrected}$ = 209.31, P < 0.798). There was, however, significant spatial correlation between p(Gond) and p(unresolved) and the correlation was negative (n = 236, Pearson’s r = -0.835, $F_{corrected}$ = 415.47, $df_{corrected}$ = 180.89, P <.001)).

Thus, as the proportion of all taxa identified from Gondwanan heritage went up, the proportion of unresolved went down, while the prop identified as Sundanian had little influence on p unresolved. This suggests that a higher proportion of unresolved species are more likely to turn out to be of Sundanian or other floristic origin than Gondwanan. The results of the present study thus presents a potentially conservative picture of the Sundanian element influence on the Queensland Wet Tropics flora. It also supports our selection of p(Gond) as opposed to p(Sundanian) as a more accurate influential factor in the model test to explain the distribution of PD.

Figure 10: Percent Gondwanan and Sundanian species per plot plotted against percent unresolved species per plot.



Elevation effects

Our results indicate that a Sundanian invasion of Australia’s wet tropical flora has been more successful in the lowlands while the high elevations and have maintained refugia for a higher percentage of endemic Australian or Gondwanan elements. The high proportion of Gondwanan or “southern affinities” in the uplands is not a new observation (Webb & Tracey 1981), but only hypotheses have been made in the past about the Sundanian component. Although the Sundanian element appears restricted by an increase in elevation, the Gondwanan although more abundant at higher elevations, also occurs at high frequencies in the lowlands.

Lowland habitats were predominant on the Sunda Plate and Southeast Asia up until about the Pliocene when New Guinea underwent a large-scale orogeny event. If phylogenetic niche conservatism was influential in the establishment of invading lineages in Australia, then northeast Queensland’s lowland habitats must have born more resemblance to the habitats of SE Asia then the uplands. The persistence of Nothofagus in the pollen record in upland sites up until the Pliocene indicates the uplands were cooler then they are today. For most of the Miocene cooler temperatures in the uplands is likely to have been a limiting factor to establishment of most invading lineages. This could explain the lack of evidence in the pollen record but also can explain the affinities of the current flora.

Previous authors have argued that invading Sundanian lineages were unlikely to have been able to compete with an already established rainforest flora in Australia, one that was gradually declining in suitable habitat as aridification swept across the continent (Adam 1992). However, periodic glacial periods forced rainforest to contract and re-expand. The re-expansion periods would have provided optimal opportunity for new invading lineages. Another possible mechanism worthy of investigation is the potential role of cyclones in enabling the establishment of foreign lineages through opening up of forest canopies on a periodic basis and potentially simultaneously providing a vector of seeds. Establishing evidence to support either of these inferred mechanisms to explain the observed patterns of PD and floristic origins data exceeds the aims of the current study and will require further investigation. The results of the present study do suggest however that the Sundanian and the Australian lowlands were similar enough to enable invading lineages to establish and compete with Australia’s native flora. Phylogenetic niche conservatism provides a plausible explanation for why the introduced lineages are more abundant in the lowlands.

CONCLUSION

A statistically significant linear relationship is identified between phylogenetic diversity and taxonomic diversity in the Queensland Wet Tropics. This relationship has been verified at multiple spatial scales and is known to have minimal sampling bias due to the utilization of a standardized plot size dataset at the smallest spatial scale (0.1

hectares). Taxonomic richness is an accurate predictor of phylogenetic diversity and thus has merit for utilization in conservation prioritization schemes. In bioregions where obtaining complete genetic sampling of all angiosperm genera is not feasible, traditional biodiversity indices based on taxonomic diversity are still valid. In the present case richness of genera accurately identifies the important areas of evolutionary history or areas with high PD. Our study shows however that in areas where obtaining sequence data for the occupant flora is possible, the hotspots that are identified by taxonomic richness can then be understood in greater depth and further prioritized if considered appropriate to do so. This builds upon the implications reported by Forest et al. (2009) from South Africa.

Regression of phylogenetic diversity data unveils hidden patterns in the landscape that can enhance our understanding of the evolutionary history of a particular bioregion. In the Queensland Wet Tropics, areas with higher PD than expected based on GR can be explained by the presence of distantly related lineages that dispersed to Australia, likely within the past five to ten million years. The collision of the Sahul (Australian) and Sunda plates is likely to have increased dispersal opportunities for plants between the regions. The remaining patches of rainforest in Australia at this time would have maintained an assembly of more cooler temperate rainforest lineages that found a pathway of dispersal into SE Asia as upland areas were created through tectonic uplift and volcanic activity. Conversely, tropical lowland rainforest was dominant in the SE Asia region at this time which would have successfully established in similar niches that opened up in the lowlands of Northern Queensland as the remnant rainforest contracted and expanded during periodic climate changes.

Phylogenetic diversity (PD) to date has been promoted primarily for its use in guiding conservation policy by identifying priority areas. Here we show that in addition to this PD can increase knowledge on the evolutionary history and biome assembly of a region when phytogeographical data is integrated. Aside from advancing the science of natural history for bioregions, this application will also give conservation planners more tools and information to utilize for management, obtaining legislative support or protection, and or applying for financial aid from different funding schemes. Although the present study, based in Queensland Wet Tropics, assesses the importance of biodiversity hotspots that are already mostly within national protected areas, the implications of these findings may prove useful in other bioregions where two or more areas are contested and must be prioritized for conservation. In this case, one would be torn with the “agony of choice” between areas that are all regarded as globally important rainforest refugia. However, by utilizing up to date tools and analyses such as demonstrated here, the preservation of different hotspot areas could be justified, each for different reasons, which could be tailored to different criteria required for conservation recognition such as World Heritage listing status or other national legislation schemes.

The lowland rainforest of tropical Northeast Queensland, is one of the most threatened forest types of the bioregion due to its suitability for agriculture and human habitation. This habitat maintains a living record of an important component of the region’s evolutionary history. It is a mixing zone between old relict lineages and more recent lineages that have dispersed and established to Australia from other continents and thus serves as an important “cradle” of new species and genetic diversity. The patterns that emerged from this study may strengthen the basis for conserving and re-vegetating more lowland habitat by emphasizing its uniqueness and importance for understanding Australia’s natural heritage and evolutionary history.

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SUPPORTING INFORMATION

Table S1: Complete list of all genera represented in phylogenetic tree and their corresponding species, sample IDs, and Voucher or GenBank Accession number.

Order	Family	Genus	Taxon	Sample ID	Voucher/Acc. No.
Austrobaileyales	Austrobaileyacea	*Austrobaileya*	*Austrobaileya scandens*	BATT943-10	Williams 5-MC10
Magnoliids					
Canellales	Winteraceae	*Bubbia*	*Bubbia queenslandiana*	BATT046-10	Costion 2094
		Tasmannia	*Tasmannia membranea*	B49	Costion 1476
Piperales	Aristolochiaceae	*Aristolochia*	*Aristolochia thozettii*	ID06	Harrington ID06
		Pararistolochia	*Pararistolochia australopithecurus*	IA07	Harrington IA07
	Piperaceae	*Peperomia*	*Peperomia hunteriana*	BATT818-10	Costion 2263
		Piper	*Piper umbellatum var. subpetalum*	E61	Costion 1803
Laurales	Atherospermataceae	*Daphnandra*	*Daphnandra repandula*	BATT428-10	Costion 1329
		Doryphora	*Doryphora aromatica*	BATT931-10	Staedler 1
		Dryadodaphne	*Dryadodaphne trachyphloia*	CERF580-11	Gray 7926
	Calycanthaceae	*Idiospermum*	*Idiospermum australiense*	D82	Hyland 7172
	Hernandiaceae	*Hernandia*	*Hernandia nymphaefolia*	BATT227-10	JGT 15283
	Lauraceae	*Beilschmiedia*	*Beilschmiedia bancroftii*	BATT437-10	Risley 334
		Cinnamomum	*Cinnamomum laubatii*	BATT423-10	Risley 327
		Cryptocarya	*Cryptocarya angulata*	BATT232-10	Costion 2082
		Endiandra	*Endiandra cowleyana*	BATT389-10	Costion 1347
		Lindera	*Lindera queenslandica*	D211	Harrington D211
		Litsea	*Litsea leefeana*	BATT473-10	Sanderson K. 1242
		Neolitsea	*Neolitsea dealbata*	SA12	Costion 2097
	Monimiaceae	*Austromattea*	*Austromattea elegans*	H66	Ford 5482
		Endressia	*Endressia wardellii*	C33	Costion 1572
		Hedycarya	*Hedycarya loxocarya*	D71	Costion 1711
		Kibara	*Kibara rigidifolia*	E43	Costion 1788
		Leviera	*Leviera acuminata*	B20	Costion 1446
		Palmeria	*Palmeria scandens*	IF10	Harrington IF10
		Stegananthera	*Stegananthera laxiflora*	BATT497-10	Costion 1570
		Wilkiea	*Wilkiea macrophylla*	CERF102-10	Ford 2879
Magnoliales	Annonaceae	*Cananga*	*Cananga odorata*	G68	Hyland 7239
		Desmos	*Desmos polycarpus*	AA H01	Costion 3107

		Fitzalania	*Fitzalania bidwillii*	AA A03	Costion 3097
		Goniothalamus	*Goniothalamus australis*	BATT907-10	Ford 4758
		Haplostichanthus	*Haplostichanthus submontanus ssp subsessilflorus*	CERF154-10	Cooper WW 2086
		Meiogyne	*Meiogyne verrycisa*	BATT214-10	GU 770
		Melodorum	*Melodorum uhrii*	IB09	Harrington IB09
		Miliusa	*Miliusa horsfieldii aff. vel.*	BATT188-10	Ford 3706
		Mitrephora	*Mitrephora zippeliana*	BATT176-10	Cooper 1466
		Murraya	*Murraya ovatifoliolata*	BATT845-10	WWC
		Polyalthia	*Polyalthia nitidissima*	BATT919-10	Ford 4967
		Pseuduvaria	*Pseuduvaria frogattii*	BATT037-10	Costion 2222
		Uvaria	*Uvaria concava*	AA G02	Costion 3108
		Xylopia	*Xylopia maccreae*	G55	Costion 1987
	Eupomatiaceae	*Eupomatia*	*Eupomatia laurina*	BATT530-10	Costion 1662
	Himantandraceae	*Galbulimima*	*Galbulimima baccata*	B29	Costion 1465
	Myristicaceae	*Horsfieldia*	*Horsfieldia australiana*	E22	Hyland 6629
		Myristica	*Myristica globosa*	BATT206-10	Costion 2136
MONOCOTS					
Alismatales	Araceae	*Alocasia*	*Alocasia brisbanensis*	BATT798-10	Gottsberger 12-091100
		Colocasia	*Colocasia esculenta*	GenBank	AM905800
		Epipremnum	*Epipremnum pinnatum*	JF03	Harrington JF03
		Gymnostachys	*Gymnostachys anceps*	BATT786-10	Ford 4711
		Pothos	*Pothos longipes*	OF6	Costion 2330
		Raphidophora	*Raphidophora australiana*	UG04	SAS 1880
		Rhaphidospora	*Rhaphidospora cavernarum*	D1812	Harrington D1812
		Typhonium	*Typhonium wilbertii*	BATT774-10	Cooper 1507
Dioscoreales	Dioscoreaceae	*Dioscorea*	*Dioscorea alata*	LH04	Harrington LH04
	Taccaceae	*Tacca*	*Tacca leontopetaloides*	BATT764-10	Fox 1678
Pandanales	Pandanaceae	*Freycinetia*	*Freycinetia scandens*	IG12	Harrington IG12
		Pandanus	*Pandanus gemmifer*	BATT544-10	Hyland 8414
	Stemonaceae	*Stemona*	*Stemona tuberosa*	GenBank	AY149350
Liliales	Philesiaceae	*Eustrephus*	*Eustrephus latifolius*	IE08	Harrington IE08
		Geitonoplesium	*Geitonoplesium cymosum*	BATT788-10	Gray 7737
	Rhipogonaceae	*Ripogonum*	*Ripogonum album*	CERF127-10	Cooper WW 2079
	Smilacaceae	*Smilax*	*Smilax glyciphylla*	D37	Costion 1677
Asparagales	Amaryllidaceae	*Crinum*	*Amaryllis*	GenBank	Z69219
		Proiphys	*Proiphys sp.*	D1814	Harrington D1814
	Asparagaceae	*Cordyline*	*Cordyline cannifolia*	CERF125-10	Zich 640
		Kuntheria	*Kuntheria pedunculata*	JA02	Harrington JA02
		Lomandra	*Lomandra sp*	LB09	Harrington LB09

		(Bellendend Ker)		
	Pleomele	*Pleomele angustifolia*	BATT847-10	Cooper 1693
	Romnalda	*Romnalda ophiopaganoidesila*	JG07	Harrington JG07
	Schelhammera	*Schelhammera multiflora*	BATT842-10	Baba 378
Boryaceae	*Borya*	*Borya septentrionalis*	D34	Costion 1680
Hemerocallidaceae	*Dianella*	*Dianella atraxis*	BATT795-10	Baba 382
Hypoxidaceae	*Molineria*	*Molineria capitualata*	JB03	Harrington JB03
Orchidaceae	*Anectochilus*	*Anectochilus yatesiae*	KA1_	Gray 8856
	Aphyllorchis	*Aphyllorchis caudata*	GenBank	FJ454873
	Apostasia	*Apostasia stylidioides*	BATT193-10	Costion 2114
	Appendicula	*Appendicula australiensis*	D1991	Harrington D1991
	Bulbophyllum	*Bulbophyllum gadgarrensis*	D1997	Harrington D1997
	Cadetia	*Cadetia taylori*	BATT210-10	Costion 2098
	Calanthe	*Calanthe vestita*	GenBank	AF074117
	Cepobacukum	*Cepobacukum trilamellatum*	D2041	Harrington D2041
	Cestichis	*Cestichis bracteata*	BATT222-10	Costion 2099
	Cheirostylis	*Pachyplectron arifolium*	GenBank	FJ571336
	Micropera	*Cleisostoma roelfeanum*	GenBank	AF074130
	Mobilabium	*Cleisostoma roelfeanum*	GenBank	AF074130
	Pomatocalpa	*Cleisostoma roelfeanum*	GenBank	AF074130
	Sarcochilus	*Cleisostoma roelfeanum*	GenBank	AF074130
	Schoenorchis	*Cleisostoma roelfeanum*	GenBank	AF074130
	Thrixspermum	*Cleisostoma roelfeanum*	GenBank	AF074130
	Pholidota	*Coelogyne cristata*	GenBank	AF074133
	Corybas	*Corybas diemenicus*	GenBank	AF074135
	Corymborkis	*Corymborkis sp.*	GenBank	AF074136
	Cymbidum	*Cymbidum madidum*	D2012	Harrington D2012
	Dendrobium	*Dendrobium fleckeri*	D1998	Harrington D1998
	Diena	*Diena montana*	D1941	Harrington D1941
	Dockrillia	*Dockrillia (Flickingeria fugax*	GenBank	D58411
	Octarrhena	*Eria ferruginea*	GenBank	AF074164
	Eria	*Eria kingii*	D2003	Harrington D2003
	Eulophia	*Eulophia nuda*	GenBank	AF074170
	Grastidium	*Grastidium baleyi*	D1947	Harrington D1947
	Peristylus	*Habenaria repens*	GenBank	AF074177
	Hetaeria	*Hetaeria agyokuana*	GenBank	HM141071
	Liparis	*Liparis liliifolia*	GenBank	AF518046
	Robiquetia	*Neofinetia falcata*	GenBank	AF074197
	Phreatia	*Phreatia sp*	GenBank	AF074214
	Plectorrhiza	*Plectorrhiza brevialis*	D2040	Harrington D2040

		Rhychophoretia	*Rhychophoretia micrantha*	D2039	Harrington D2039
		Zeuxine	*Zeuxine (Goodyera repens)*	GenBank	FJ571330
Commelinids					
Arecales	Arecaceae	*Archontophoenix*	*Archontophoenix alexandrae*	BATT073-10	Costion 2228
		Arenga	*Arenga australasica*	G41	Costion 1985
		Calamus	*Calamus moti*	UB01	SAS 1780
		Cocos	*Cocos nucifera*	GenBank	AY012507
		Hydriastele	*Hydriastele wendlandiana*	AA B02	Costion 3099
		Laccospadix	*Laccospadix australasica*	C55	Costion 1587
		Licuala	*Licuala ramsayi*	BATT061-10	Costion 2227
		Linospadix	*Linospadix sp.*	JA12	Harrington JA12
		Livistona	*Livistona benthamii*	BATT713-10	IRVINE
		Normanbayi	*Normanbayi normanbayi*	BATT609-10	Costion 1917
		Oraniopsis	*Oraniopsis apendiculata*	BATT691-10	Costion 1586
		Ptychosperma	*Ptychosperma elegans*	BATT718-10	IRV 1008
Commelinales	Commelinaceae	*Aneilema*	*Aneilema acuminata*	BATT145-10	Gray 7954
		Commelina	*Commelina ensifolia*	KH05	Gray 7946
		Pollia	*Pollia hassakarlii*	GenBank	AF312262
	Philydraceae	*Helmholtzia*	*Helmholtzia acorifolia*	CERF134-10	Harrington M 358
Poales	Cyperaceae	*Carex*	*Carex horsfieldii*	BATT098-10	Forster 25917
		Cyperus	*Cyperus decompositus*	NH01	Gray 7227
		Cyperus	*Cyperus gracilis*	XB11	SAS 672
		Exocarya	*Exocarya scleroides*	BATT327-10	Ford 1863
		Gahnia	*Gahnia javanica*	GenBank	Y12973
		Hypolytrum	*Hypolytrum nemorum*	BATT303-10	Jago B. 1335
		Lepidosperma	*Lepidosperma tortuosum*	GenBank	AY725950
		Mapania	*Mapania macrocephala*	BATT363-10	Ford 4594
		Paramapania	*Paramapania parvibracteata*	BATT315-10	Ford 4541
		Rhynchospora	*Rhynchospora corymbosa*	BATT351-10	Gray 6546
		Scleria	*Scleria brownii*	BATT339-10	Gray 8057
	Flagellariaceae	*Flagellaria*	*Flagellaria indica*	IG08	Harrington IG08
	Poaceae	*Ancistrachne*	*Ancistrachne uncinulata*	BATT362-10	Gray 8476
		Centotheca	*Centotheca lappacea*	BATT811-10	Ford 5281
		Crytococcum	*Crytococcum oxyphyllum*	BATT183-10	Ford 5240
		Entolasia	*Entolasia stricta*	BATT350-10	Ford 3575
		Garnotia	*Garnotia stricta*	BATT338-10	Ford 3006
		Ichananthus	*Ichananthus pallens var. majus*	BATT171-10	Ford 4993

		Leptasis	*Leptasis banksii*	BATT799-10	Ford 3888
		Lophatherum	*Lophatherum gracile*	BATT787-10	Ford 4999
		Microlaena	*Microlaena stipoides*	BATT159-10	Ford 3765
		Mullerochloa	*Mullerochloa moreheadiana*	BATT147-10	Ford 4893
		Neololeba	*Neololeba atra*	BATT135-10	Waterhouse 7163
		Oplismenus	*Oplismenus compositus*	BATT319-10	Ford 5289
		Ottochloa	*Ottochloa nodosa*	NC03	Ford 5072
		Panicum	*Panicum mitchellii*	BATT111-10	Hyland 12789
		Pogonatherum	*Pogonatherum crinitum*	BATT099-10	Ford 3004
		Sacciolepis	*Sacciolepis indica*	BATT835-10	Mckenna 294
		Setaria	*Setaria palmifolia*	GenBank	AM849389
		Thuarea	*Thuarea (Ischaemum*	GenBank	AM849411
Zingiberales	Costaceae	*Costus*	*Costus potierae*	IH09	Harrington IH09
	Musaceae	*Musa*	*Musa banksii*	E50	Costion 1797
	Zingiberaceae	*Alpinia*	*Alpinia modesta*	BATT834-10	Gray 6665
		Amomum	*Amomum dallachy*	BATT822-10	Ford 3806
		Curcuma	*Curcuma australasica*	BATT810-10	Gray 7997
		Hornstedtia	*Hornstedtia scottiana*	BATT291-10	Gray 6521
		Pleuranthodium	*Riedelia sp.*	GenBank	AF243849
		Tapeinochilos	*Tapeinochilos ananassae*	E30	Costion 1815
EUDICOTS					
Ranunculales	Menispermaceae	*Carronia*	*Carronia protensa*	BATT236-10	Costion 2233
		Hypserpa	*Hypserpa smilacifolia*	D11	Costion 1654
		Legnephora	*Legnephora moorei*	BATT137-10	Forster 34434
		Pachygone	*Pachygone ovata*	IH12	Harrington IH12
		Parapachygone	*Parapachygone longiflora*	BATT125-10	Ford 5230
		Pleogyne	*Pleogyne australis*	KH11	Ford 3458
		Pycnarrhena	*Pycnarrhena novoguineensis*	BATT369-10	Gray 8794
		Sarcopetalum	*Sarcopetalum harveyanum*	GenBank	FJ026504
		Stephania	*Stephania japonica*	BATT525-10	Costion 1653
		Tinospora	*Tinospora smilacina*	BATT101-10	Gray 8798
	Ranunculaceae	*Clematis*	*Clematis pickeringii*	XD06	SAS 232
Proteales	Proteaceae	*Alloxylon*	*Alloxylon wickhamii*	BATT064-10	Costion 1319
		Athertonia	*Athertonia diversifolia*	F88	JC 1
		Austromuellera	*Austromuellera trinervia*	BATT890-10	Ford 4849
		Banksia	*Banksia aquilonia*	D30	Costion 1668
		Buckinghamia	*Buckinghamia celsissima*	BATT625-10	Costion 1955
		Cardwellia	*Cardwellia sublimis*	BATT439-10	Sanderson K. 54
		Carnarvonia	*Carnarvonia araliifolia var. montana*	BATT651-10	Costion 2030

		Catalepidia	*Catalepidia heyana*	C17	Costion 1552
		Darlingia	*Darlingia darlingiana*	BATT591-10	Costion 1881
		Eidothea	*Eidothea zoexylocarya*	AA F2	Costion & Sankowsky 3105
		Gevuina	*Gevuina bleasdalei*	G06	Costion 1940
		Grevillea	*Grevillea baileyana*	E02	JC 5
		Helicia	*Helicia australasica*	BATT669-10	Costion 1380
		Hicksbeachia	*Hicksbeachia pilosa*	AA C03	Costion 3104
		Hollandaea	*Hollandaea sayeriana*	D47	Costion 1683
		Lomatia	*Lomatia fraxinifolia*	BATT447-10	Costion 1449
		Lasjia	*Macadamia caludiensis*	D69	RFK 3102
		Macaranga	*Macaranga inamoena*	BATT678-10	Costion 1473
		Megahertzia	*Megahertzia amplexicaulis*	BATT728-10	RFK 3196
		Musgravea	*Musgravea heterophylla*	BATT508-10	Sanderson K. 1041
		Neorites	*Neorites kevidiana*	BATT693-10	Costion 1631
		Opisthiolepis	*Opisthiolepis heterophylla*	BATT671-10	Sanderson K. 58
		Orites	*Orites myrtoidea*	GenBank	DQ875842
		Placospermum	*Placospermum coriaceum*	C05	Sanderson, K. 433
		Sphalmium	*Sphalmium racemosum*	BATT686-10	Sanderson K. 461
		Stenocarpus	*Stenocarpus davallioides*	BATT008-10	Costion 1576
		Triunia	*Triunia youngiana*	GenBank	DQ875841
Core eudicots					
Dilleniales	Dilleniaceae	*Dillenia*	*Dillenia alata*	BATT608-10	Costion 1918
		Hibbertia	*Hibbertia scandens*	D27	Costion 1671
		Tetracera	*Tetracera daemeliana*	BATT259-10	Costion 2160
Saxifragales	Hamamelidaceae	*Neostrearia*	*Neostrearia fleckeri*	OA05	PIF 25923
		Noahdendron	*Noahdendron nicholasii*	WF04	Costion 2964
		Ostrearia	*Ostrearia australiana*	BATT734-10	JC 22
Santalales	Loranthaceae	*Amyema*	*Amyema villiflorum subsp. tomentillum*	C59	Costion 1601
		Amylotheca	*Amylotheca dictyophleba*	D40	Costion 1674
		Decaisnina	*Decaisnina triflora*	GenBank	EU544468
		Dendrophtoe	*Dendrophtoe vitellina*	B12	Costion 1437
		Diplatia	*Diplatia furcata*	BATT122-10	Ford 4720
		Loranthaceae	*Loranthaceae*	H56	Costion 2075
	Olacaceae	*Ximenia*	*Ximenia americana*	C60	Costion 1600
	Opiliaceae	*Cansjera*	*Cansjera leptostachya*	GenBank	DQ790128
		Opilia	*Opilia amentaea*	BATT524-10	Costion 1656
	Santalaceae	*Exocarpos*	*Exocarpos latifolium*	BATT865-10	Fox 1639

		Korthalsella	*Korthalsella grayi*	LG09	Harrington LG09
		Notothixos	*Notothixos subaureus*	B30	Costion 1455
		Santalum	*Santalum lanceolatum*	BATT852-10	Forster 23663
		Viscum	*Viscum articulatum*	BATT450-10	Costion 1456
Caryophyllales	Amaranthaceae	*Achyranthes*	*Achyranthes aspera*	BATT173-10	Fox 2502
		Deeringia	*Deeringia amaranthoides*	BATT161-10	Cooper 1336
	Droseraceae	*Drosera*	*Drosera prolifera*	BATT770-10	Ford 5312
	Nyctaginaceae	*Pisonia*	*Pisonia umbelliflora*	E54	Costion 1793
	Polygonaceae	*Muehlenbeckia*	*Muehlenbeckia complexa*	GenBank	FM883619
		Persicaria	*Persicaria barbata*	BATT805-10	Addicott 1203
Rosids					
Vitales	Vitaceae	*Ampelocissus*	*Ampelocissus thyrsiflora*	GenBank	AJ402919
		Cayratia	*Cayratia saponaria*	JA05	Harrington JA05
		Cissus	*Cissus hypoglauca*	BATT703-10	Costion 1670
		Clematicissus	*Clematicissus angustissima*	GenBank	AJ419728
		Leea	*Leea indica*	BATT743-10	Costion 1810
		Tetrastigma	*Tetrastigma trifoliolatum*	GenBank	AJ419716
Eurosids I					
Celastrales	Celastraceae	*Cassine*	*Cassine melanocarpa*	A46	Costion 1385
		Celastrus	*Celastrus subspicatus*	BATT838-10	Ford 4994
		Denhamia	*Denhamia viridissima*	C22	Sanderson, K. 476
		Elaeodendron	*Elaeodendron melanocarpum*	E25	Hyland 11352
		Euonymus	*Euonymus globularis*	BATT826-10	Ford 4739
		Hedraianthera	*Hedraianthera porphyropetala*	BATT948-10	Ford 4562
		Hexaspora	*Hexaspora pubescens*	BATT170-10	Gray 7633
		Hippocratea	*Hippocratea barbata*	BATT284-10	Costion 2183
		Hypsophila	*Hypsophila dielsiana*	D32	Costion 1666
		Maytenus	*Maytenus disperma*	D83	Gray 344
		Perrottetia	*Perrottetia arborescens*	D52	Costion 1696
		Salacia	*Salacia chinensis*	JH06	Harrington JH06
		Siphonodon	*Siphonodon membranaceus*	BATT119-10	Costion 2215
Oxalidales	Connaraceae	*Connarus*	*Connarus conchocarpus*	GenBank	L29493.2
	Connaraceae	*Rourea*	*Rourea brachyandra*	BATT331-10	Ford 5402
	Cunoniaceae	*Acsmithia*	*Acsmithia davidsonii*	D70	Costion 1712
		Caldcluvia	*Caldcluvia paniculata*	GenBank	AF291922
		Ceratopetalum	*Ceratopetalum succirubrum*	A93	Sanderson, K. 137
		Davidsonia	*Davidsonia pruriens*	A60	Risley 359
		Geissois	*Geissois biagiana*	G70	Costion 2004
		Gillbeea	*Gillbeea adenophila*	BATT154-10	Costion 2179

		Pseudoweinmannia	*Pseudoweinmannia lachnocarpa*	A39	Costion 1376
		Pullea	*Pullea stutzeri*	BATT628-10	Costion 1964
		Schizomeria	*Schizomeria whitei*	AA C02	Costion 3103
	Elaeocarpaceae	*Aceratium*	*Aceratium ferrugineum*	BATT690-10	Costion 1590
		Elaeocarpus	*Elaeocarpus bancroftii*	BATT930-10	Crayn 861
		Peripentadenia	*Peripentadenia phelpsii*	AA A01	Costion 3089
		Sloanea	*Sloanea australis ssp parviflora*	BATT106-10	Costion 2255
Malpighiales	Balanopaceae	*Balanops*	*Balanops australiana*	BATT418-10	Sanderson K. 78
	Clusiaceae	*Calophyllum*	*Calophyllum sil*	RE08	Costion 2639
		Garcinia	*Garcinia sp.*	BATT758-10	Costion 1886
		Mammea	*Mammea siamensis*	GenBank	AY625028
		Mesua	*Mesua sp.*	BATT706-10	Costion 1701
	Dichapetalaceae	*Dichapetalum*	*Dichapetalum papuanum*	BATT888-10	Ford 4796
	Erythroxylaceae	*Erythroxylum*	*Erythroxylum ecarinatum*	BATT432-10	Costion 1352
	Euphorbiaceae	*Alchorne*	*Alchorne thozetiana*	F79	Costion 1915
		Aleurites	*Aleurites molucannus*	BATT856-10	JC 17
		Baloghia	*Baloghia parviflora*	BATT519-10	Costion 1634
		Claoxylon	*Claoxylon tenerifolium*	RE09	Ford 4410
		Cleidion	*Cleidion javanicum*	D94	Hyland 9540
		Codiaeum	*Codiaeum variegatum*	BATT667-10	Costion 1363
		Croton	*Croton insularis*	BATT668-10	Costion 1374
		Dimorphocalyx	*Dimorphocalyx austaliensis*	IA12	Harrington IA12
		Endospermum	*Endospermum myrmecophilum*	BATT864-10	Waterhouse 7306
		Excoecaria	*Excoecaria agallocha*	GenBank	AY794839
		Fontainea	*Fontainea picrosperma*	D42	Costion 1689
		Homalanthus	*Homalanthus novoguineensis*	CERF164-10	Crayn 1177
		Hylandia	*Hylandia dockrillii*	C18	Costion 1551
		Mallotus	*Mallotus mollisimus*	BATT731-10	Hyland 11482
		Omphalea	*Omphalea queenslandiae*	CERF122-10	Harrington M 368
		Rockinghamia	*Rockinghamia angustifolia*	BATT440-10	Risley 381
		Tragia	*Tragia urticifolia*	GenBank	AY794925
		Wetria	*Wetria australiensis*	H63	Hyland 25942
	Linaceae	*Hugonia*	*Hugonia jenkinsii*	AA E1	Costion & Sankowsky 3098
	Ochnaceae	*Brackenridgea*	*Brackenridgea australiana*	BATT757-10	Costion 1874
	Passifloraceae	*Adenia*	*Adenia heterophylla*	BATT806-10	Ford 4472
	Passifloraceae	*Passiflora*	*Passiflora kuranda*	BATT248-10	Costion 2230
	Phyllanthaceae	*Actephila*	*Actephila foetida*	BATT821-10	Gray 5881

		Antidesma	*Antidesma bunius*	BATT730-10	RIS 113
		Bischofia	*Bischofia javanica*	WC10	Costion 3012
		Breynia	*Breynia stipitata*	BATT521-10	Costion 1646
		Bridelia	*Bridelia tomentosa*	CERF126-10	Hyland B 16828
		Cleistanthus	*Cleistanthus hylandii*	D89	JC 20
		Flueggea	*Flueggea leucopyros*	XA02	SAS 440
		Glochidion	*Glochidion harvieanum*	BATT010-10	Costion 1811
		Margaritaria	*Margaritaria tetracocca*	GenBank	Z75675
		Phyllanthus	*Phyllanthus lamprophyllus*	BATT831-10	Baba 404
		Sauropus	*Sauropus macranthus*	A25	Costion 1362
	Picrodendraceae	*Austrobuxus*	*Austrobuxus megacarpus*	C10	Sanderson, K. 472
		Choriceras	*Choriceras tricorne*	BATT542-10	Costion 1745
		Dissiliaria	*Dissiliaria surculosa*	BATT832-10	Costion 1991
		Sankowskya	*Sankowskya stipularis*	AA A02	Costion 3094
		Whyanbeelia	*Whyanbeelia terrae-reginae*	BATT833-10	Forster 17171
	Putranjavaceae	*Drypetes*	*Drypetes sp.*	BATT809-10	Ford 2673
	Rhizophoraceae	*Carallia*	*Carallia brachiata*	E56	Costion 1791
		Lumnitzera	*Lumnitzera sp.*	C57	Costion 1603
	Salicaceae	*Baileyoxylon*	*Baileyoxylon lanceolatum*	BATT705-10	Costion 1700
		Casearia	*Casearia costulata*	BATT529-10	Costion 1664
		Flacourtia	*Flacourtia sp. (Shipton)*	H86	WCRJ H86
		Homalium	*Homalium circumpinnatum*	BATT068-10	Costion 1612
		Ryparosa	*Ryparosa javanica*	BATT019-10	Costion 1517
		Scolopia	*Scolopia braunii*	D93	WIF 624
		Xylosma	*Xylosma terrae-reginae*	BATT797-10	RJ 1720
Cucurbitales	Corynocarpaceae	*Corynocarpus*	*Corynocarpus cribbianus*	BATT081-10	Costion 1802
	Cucurbitaceae	*Diplocyclos*	*Diplocyclos palmatus*	XG03	SAS 781
		Momordica	*Momordica cochinchinensis*	LF01	Harrington LF01
		Neoachmandra	*Neoachmandra cunninghamia*	BATT109-10	Ford 3420
		Neoalsomitra	*Neoalsomitra trifoliolata*	BATT841-10	Ford 3796
		Trichosanthes	*Trichosanthes pentaphylla*	BATT853-10	Gray 7762
		Zehrnia	*Zehrnia mucronata*	BATT185-10	Forster 23042
Fabales	Fabaceae	*Abrus*	*Abrus precatorius*	BATT779-10	Hyland 15764
		Acacia	*Acacia celsa*	BATT433-10	Sanderson K. 259
		Adenanthera	*Adenanthera pavonina*	BATT867-10	Ford 4372
		Albizia	*Albizia sp.*	BATT250-10	KS 1810
		Archidendron	*Archidendron grandiflorum*	BATT926-10	Gray 7863

		Archidendropsis	*Archidendropsis sp.*	OC05	Ford 3595
		Austrosteenisia	*Austrosteenisia sp.*	BATT243-10	Costion 2123
		Caesalpinia	*Caesalpinia traceyi*	BATT272-10	Costion 2181
		Callerya	*Callerya pilipes*	YG10	Costion 3191
		Calopogonium	*Calopogonium mucunoides*	BATT791-10	Ford 4701
		Canavalia	*Canavalia papuana*	BATT121-10	Fox 1067
		Cassia	*Cassia queenslandica*	LE07	Harrington LE07
		Castanospermum	*Castanospermum australe*	BATT382-10	Costion 1334
		Cynometra	*Cynometra iripa*	BATT851-10	Gray 8933
		Derris	*Derris trifoliata*	LD07	Harrington LD07
		Desmodium	*Desmodium tortuosum*	BATT815-10	Sankowsky 1665
		Dioclea	*Dioclea hexandra*	KF09	Ford 5278
		Entada	*Entada phaseoloides*	BATT247-10	Costion 2163
		Erythrina	*Erythrina variegata*	F87	Hyland 12440
		Erythrophleum	*Erythrophleum chlorostachys*	IC12	Harrington IC12
		Flemingia	*Flemingia parviflora*	BATT320-10	Forster 22813
		Intsia	*Intsia bijuga*	TG12	Costion & Schulte 2898
		Maniltoa	*Maniltoa lenticellata*	BATT784-10	Costion 1929
		Millettia	*Millettia pinnata*	BATT717-10	IRV 664
		Mucuna	*Mucuna pruriens*	GenBank	DUH 13260
		Ormosia	*Ormosia ormondii*	G65	Costion 2009
		Pararchidendron	*Pararchidendron pruinosum*	BATT761-10	Costion 1912
		Paraserianthes	*Paraserianthes toona*	BATT792-10	Gray 7627
		Rhynchosia	*Rhynchosia minima*	BATT332-10	Gray 7546
		Senna	*Senna coronilloides*	BATT780-10	Hyland 15522
		Storckiella	*Storckiella australiensis*	B83	Costion 1513
		Vandasina	*Vandasina retusa*	BATT839-10	Ford 4706
		Vigna	*Vigna unguiculata*	GenBank	EU717266
	Xanthophyllaceae	*Xanthophyllum*	*Xanthophyllum octandrum*	BATT588-10	Costion 1870
Fagales	Casuarinaceae	*Gymnostoma*	*Gymnostoma australianum*	H76	Ford H76
		Allocausarina	*Allocausarina torlosa*	F84	IRV 734
		Casuarina	*Casuarina equisetifolia*	GenBank	AY263930
Rosales	Elaeagnaceae	*Elaeagnus*	*Elaeagnus triflora*	BATT738-10	Costion 1807
	Moraceae	*Antiaris*	*Antiaris toxicaria*	BATT205-10	RFK 2927
		Ficus	*Ficus destruens*	CERF135-10	Worboys SJ 805
		Maclura	*Maclura pomifera*	GenBank	D86318
		Streblus	*Streblus glaber var. australiensis*	BATT434-10	Risley 369
		Trophis	*Trophis scandens*	BATT200-10	Costion 2241
	Rhamnaceae	*Alphitonia*	*Alphitonia excelsa*	D24	Costion 1657
		Colubrina	*Colubrina asiatica*	D21	Costion 1660
		Emmenosperma	*Emmenosperma alphitonioides*	F80	Gray 3325

		Gouania	*Gouania australiana*	LA05	Harrington LA05
		Rhamnella	*Rhamnella vitensis*	BATT296-10	Ford 4872
		Sageretia	*Sageretia hamosa*	KG09	Ford 5248
		Schistocarpaea	*Schistocarpaea johnsonii*	D63	Costion 1702
		Ventilago	*Ventilago viminalis*	GenBank	AJ390035
	Rosaceae	*Prunus*	*Prunus turneriana*	BATT143-10	Costion 2221
		Rubus	*Rubus queenslandicus*	BATT310-10	Ford 2125
	Ulmaceae	*Aphananthe*	*Aphananthe philippinensis*	BATT886-10	Ford 3111
		Celtis	*Celtis paniculata*	BATT898-10	Bean 16205
		Trema	*Trema orientalis*	WC07	Costion 2985
	Urticaceae	*Boehmeria*	*Boehmeria nivea*	GenBank	AF062005
		Dendrocnide	*Dendrocnide photinophylla*	BATT016-10	Costion 1313
		Elatostema	*Elatostema reticulatum*	BATT149-10	Gray 8327
		Pipturus	*Pipturus argenteus*	C71	Costion 1605
		Pouzolzia	*Pouzolzia zeylanica*	BATT345-10	Ford 4853
		Procris	*Procris pedunculata*	KD11	Harrington KD11
Eurosids II					
Myrtales	Combretaceae	*Macropteranthes*	*Macropteranthes montana*	BATT750-10	Costion 1841
		Terminalia	*Terminalia sericocarpa*	B87	Costion 1518
	Lythraceae	*Lagerstroemia*	*Lagerstroemia archeriana*	E20	RFK 2543
	Melastomataceae	*Medinilla*	*Medinilla sp.*	GenBank	AB586402
		Melastoma	*Melastoma affine*	BATT255-10	Costion 2124
		Memecylon	*Memecylon pauciflorum*	BATT844-10	Hyland 9494
	Myrtaceae	*Acmena*	*Acmena resa*	C51	Costion 1591
		Acmenosperma	*Acmenosperma claviflorum*	BATT424-10	Costion 1312
		Archidomyrtus	*Archidomyrtus beckleri*	OF05	PIF 24020
		Austromyrtus	*Austromyrtus hillii*	A32	Costion 1369
		Backhousia	*Backhousia enata*	BATT610-10	Ford 3780
		Callistemon	*Callistemon viminalis*	BATT639-10	Costion 2001
		Corymbia	*Corymbia torrelliana*	G50	RIS 167
		Decaspermum	*Decaspermum humile*	A38	Costion 1375
		Eucalyptus	*Eucalyptus pellita*	F85	IRV 227
		Eugenia	*Eugenia sp.*	UH07	Costion 2757
		Gossia	*Gossia shepherdii*	BATT739-10	Costion 1806
		Lenwebbia	*Lenwebbia lasioclada*	KG06	Ford 5412
		Leptospermum	*Leptospermum wooroonooran*	CERF158-10	Crayn 1172
		Lindsayomyrtus	*Lindsayomyrtus racemoides*	BATT729-10	Hyland 6607
		Lithomyrtus	*Lithomyrtus obtusa*	JG02	Harrington JG02
		Lophostemon	*Lophostemon suaveolens*	G59	Hyland 11406

		Melaleuca	*Melaleuca stenostachya*	F86	Hyland 7710
		Pilidiostigma	*Pilidiostigma sessile*	BATT251-10	Ford 3239
		Rhodamnia	*Rhodamnia blairiana*	BATT913-10	Ford 4971
		Rhodomyrtus	*Rhodomyrtus macrocarpa*	UH06	Costion 2752
		Ristantia	*Ristantia gouldii*	D67	Hyland 7193
		Sphaerantia	*Sphaerantia discolor*	D84	Gray 848
		Stockwellia	*Stockwellia quadrifida*	D57	Costion 1708
		Syncarpia	*Syncarpia glomulifera*	AA D01	Costion 3088
		Syzygium	*Syzygium kuranda*	BATT537-10	Hyland 6778
		Thaleropia	*Thaleropia queenslandica*	D65	Hyland 6683
		Tristaniopsis	*Tristaniopsis exiliiflora*	IB11	Harrington IB11
		Uromyrtus	*Uromyrtus metrosideros*	GenBank	AM235661
		Waterhousea	*Waterhousea unipunctata*	BATT599-10	Costion 1905
		Xanthostemon	*Xanthostemon whitei*	B59	Unwin 696
	Onagraceae	*Ludwigia*	*Ludwigia hyssopifolia*	GenBank	AY036152
Brassicales	Capparaceae	*Capparis*	*Capparis aborescens*	C58	Costion 1602
Malvales	Bixaceae	*Cochlospermum*	*Cochlospermum gillivraei*	BATT023-10	Costion 2126
		Coelospermum	*Coelospermum sp. (Boonjee)*	D72	Costion 1710
	Malvaceae	*Abelmoschus*	*Abelmoschus moschus*	PB09	Clarkson 8732
		Abroma	*Abroma angusta*	GenBank	AJ012208
		Abutilon	*Abutilon oxycarpon*	RA12	Ford 4760
		Argyrodendron	*Argyrodendron peralatum*	BATT093-10	Costion 1812
		Bombax	*Bombax ceiba var. leiocarpum*	D92	Hyland 11133
		Brachychiton	*Brachychiton acerifolius*	BATT442-10	Sanderson K. 238
		Commersonia	*Commersonia bartramia*	BATT306-10	Ford 5286
		Firmiana	*Firmiana papuana*	BATT859-10	Ford 4799
		Franciscodendron	*Franciscodendron laurifolium*	BATT268-10	Costion 2085
		Grewia	*Grewia papuana*	RG11	Gray 8483
		Helicteres	*Helicteres isora*	JD09	Harrington JD09
		Heritiera	*Heritiera littoralis*	BATT550-10	JC 129
		Hibiscus	*Hibiscus tiliaceus*	D79	Gray 2188
		Kleinhovia	*Kleinhovia hospita*	BATT286-10	Ford 4726
		Sterculia	*Sterculia quadrifida*	E03	IRV 683
		Thespesia	*Thespesia populneoides*	F64	Costion 1898
		Trichospermum	*Trichospermum pleiostigma*	OE05	Ford 4942

		Abroma	*Abroma angusta*	GenBank	AJ012208
	Thymelaeaceae	*Lethedon*	*Lethedon setosa*	BATT057-10	Costion 1709
		Oreodendron	*Oreodendron biflorum*	C41	Costion 1584
		Phaleria	*Phaleria octandra*	BATT925-10	Hyland 15468
		Wikstromia	*Wikstromia indica*	C89	Costion 1639
Sapindales	Anacardiaceae	*Blepharocarya*	*Blepharocarya involucrigera*	B15	Sanderson, K. 245
		Buchanania	*Buchanania arborescens*	JC10	Harrington JC10
		Euroschinus	*Euroschinus falcata*	BATT018-10	Costion 1360
		Pleiogynium	*Pleiogynium timorense*	E46	AD 992
		Rhus	*Rhus taitensis*	G76	Costion 2014
		Semecarpus	*Semecarpus australiensis*	E40	Hyland 11660
	Burseraceae	*Canarium*	*Canarium australasicum*	BATT655-10	Costion 2036
		Garuga	*Garuga floribunda*	MG02	Hyland 11522
	Meliaceae	*Aglaia*	*Aglaia argentea*	CERF180-10	FRI Chung 39475
		Anthocarpa	*Anthocarpa nitidula*	CERF172-10	Jensen 950
		Chisocheton	*Chisocheton longistipitatus*	E71	Costion 1809
		Dysoxylum	*Dysoxylum gaudichaudianum*	BATT721-10	RFK 2825
		Melia	*Melia azedarach*	D10	Costion 1655
		Synoum	*Synoum muelleri*	C06	Sanderson, K. 434
		Toona	*Toona ciliata*	BATT602-10	Costion 1913
		Turraea	*Turraea pubescens*	BATT778-10	Gray 9051
		Vavaea	*Vavaea amicorum*	E27	JC 33
	Rutaceae	*Acronychia*	*Acronychia acidula*	A66	Sanderson, K. 59
		Bosistoa	*Bosistoa medicinalis*	BATT038-10	Costion 1285
		Brombya	*Brombya platynema*	BATT036-10	Costion 2200
		Citrus	*Citrus garrawayae*	BATT716-10	RFK 2845
		Clausena	*Clausena brevistyla*	SF04	Gray 7082
		Dinosperma	*Dinosperma erythrocca*	A35	Costion 1372
		Euodia	*Euodia hylandii*	B82	Costion 1512
		Flindersia	*Flindersia bourjotiana*	BATT749-10	Costion 1831
		Geijera	*Geijera salicifolia*	SB03	IDF 1100
		Glycosmis	*Glycosmis trifoliata*	BATT283-10	Costion 2242
		Halfordia	*Halfordia kendack*	BATT629-10	Costion 1963
		Leionema	*Leionema ellipticum*	H88	Ford 2262
		Medicosma	*Medicosma fareana*	BATT467-10	Sanderson K. 1238
		Melicope	*Melicope vitiflora*	BATT697-10	Costion 1632
		Micromelum	*Micromelum minutum*	BATT692-10	Costion 1611
		Pitaviaster	*Pitaviaster haplophyllus*	BATT090-10	Costion 1555
		Sarcomelicope	*Sarcomelicope simplicifolia*	A44	Costion 1382
		Zanthoxylum	*Zanthoxylum*	BATT699-10	Costion 1644

			ovalifolium		
		Zieria	*Zieria madida*	D25	Costion 1673
	Sapindaceae	*Alectryon*	*Alectryon connatus*	SC3	Ford 2045
		Allophyllus	*Allophyllus cobbe*	AA C03	Costion 3119
		Arytera	*Arytera pauciflora*	H35	Costion 2071
		Atalaya	*Atalaya sericopetala*	H49	Ford 2296
		Castanospora	*Castanospora alphandii*	KH09	Ford 4800
		Cnesmocarpon	*Cnesmocarpon dasyantha*	A51	Sanderson, K. 85
		Cupaniopsis	*Cupaniopsis foeveolata*	BATT820-10	Costion 1983
		Diploglottis	*Diploglottis smithii*	TA12	Jago, B. 374
		Elattostachys	*Elattostachys microcarpa*	TA10	Ford 5395
		Ganophyllum	*Ganophyllum falcatum*	UD03	SAS 1902
		Guioa	*Guioa acutifolia*	TF09	Jones 18986
		Harpullia	*Harpullia rhyticarpa*	BATT498-10	Costion 1567
		Jagera	*Jagera sp.*	BATT204-10	Costion 2105
		Lepiderema	*Lepiderema largiflorens*	H57	Ford 2962
		Mischarytera	*Mischarytera lautereriana*	BATT650-10	Costion 2031
		Mischocarpus	*Mischocarpus albescens*	BATT785-10	Ford 4000
		Rhysotoechia	*Rhysotoechia florulenta*	CERF163-10	Ford 5409
		Sarcopteryx	*Sarcopteryx reticulata*	BATT011-10	Costion 2112
		Sarcotoechia	*Sarcotoechia cuneata*	BATT654-10	Costion 2037
		Synima	*Synima reynoldsiae*	B52	Costion 1479
		Toechima	*Toechima erythrocarpum*	BATT515-10	Costion 1484
	Simaroubaceae	*Ailanthus*	*Ailanthus triphysa*	BATT643-10	Costion 2008
		Brucea	*Brucea javanica*	LF07	Harrington LF07
		Quassia	*Samadera baileyana*	BATT683-10	Costion 1514
Asterids					
Cornales	Cornaceae	*Alangium*	*Alangium villosum var. polyosmoides*	A67	Sanderson, K. 53
Ericales	Actinidiaceae	*Saurauia*	*Saurauia andreana*	D43	Costion 1688
	Ebenaceae	*Diospyros*	*Diospyros hebecarpa*	BATT540-10	RFK 2751
	Ericaceae	*Acrothamnus*	*Acrothamnus spathaceus*	YD04	Worboys 835
		Dracophyllum	*Dracophyllum sayeri*	CERF170-10	Crayn 1155
		Leucopogon	*Leucopogon spathaceus*	C54	Costion 1588
		Paphia	*Paphia meiniana*	CERF156-10	Crayn 1176
		Rhododendron	*Rhododendron grande*	GenBank	GU176646
		Trochocarpa	*Trochocarpa bellendenkerensis*	JE09	Harrington JE09
	Lecythidaceae	*Barringtonia*	*Barringtonia calyptrata*	BATT736-10	Costion 1795

		Planchonia	*Planchonia careya*	F63	Costion 1899
	Primulaceae	*Ardisia*	*Ardisia pachyrrhachis*	BATT523-10	Costion 1640
		Embelia	*Embelia australiana*	AA E12	Costion 3178
		Maesa	*Maesa dependens*	BATT535-10	Costion 1692
		Myrsine	*Myrsine achradifolia*	BATT808-10	Costion 1936
		Rapanea	*Rapanea achradifolia*	BATT682-10	Costion 1495
	Primulaceae	*Tapeinosperma*	*Tapeinosperma pallidum*	C42	Costion 1583
	Sapotaceae	*Chrysophyllum*	*Chrysophyllum roxburghii*	BATT725-10	Hyland 6397
		Manilkara	*Manilkara elengi*	C62	Costion 1598
		Mimusops	*Mimusops elengi*	D66	GS 992
		Niemeyera	*Niemeyera prunifera*	C93	Costion 1635
		Palaquium	*Palaquium glactoxylon*	YC09	Costion 2154
		Planchonella	*Planchonella euphlebia*	BATT484-10	Sanderson K. 435
		Pouteria	*Pouteria pearsoniorum*	C11	Sanderson, K. 470
		Sersalisia	*Sersalisia sessiliflora*	C19	Costion 1549
		Vanroyena	*Vanroyena castanosperma*	BATT366-10	Gray 6534
	Symplocaceae	*Symplocos*	*Symplocos ampulliformis*	CERF162-10	Zich CostionF7
	Theaceae	*Ternstroemia*	*Ternstroemia cherryi*	A01	Costion 1333
Euasterids I					
Unplaced	Boraginaceae	*Cordia*	*Cordia dichotoma*	BATT727-10	Gray 1870
		Ehretia	*Ehretia laevis*	H71	RLJ 5222
		Heliotropium	*Heliotropium sp.*	AA F03	Costion 3102
	Icacinaceae	*Apodytes*	*Apodytes brachystylis*	BATT177-10	Costion 2257
Gentianales	Apocynaceae	*Alstonia*	*Alstonia muelleriana*	B14	Sanderson, K. 246
		Alyxia	*Alyxia spicata*	BATT526-10	Costion 1650
		Carissa	*Carissa ovata*	BATT849-10	Forster 25425
		Cerbera	*Cerbera floribunda*	E33	Hyland 8479
		Dischidia	*Dischidia nummularia*	BATT270-10	Costion 2131
		Gymnanthera	*Gymnanthera oblonga*	BATT801-10	Ford 2607
		Heterostemma	*Heterostemma acuminatum*	BATT813-10	Holmes 161
		Hoya	*Hoya australis ssp. Tenuipes*	BATT199-10	Costion 2133
		Ichnocarpus	*Ichnocarpus frutescens*	OE06	Baba 364
		Kopsia	*Kopsia arborea*	OA06	Ford 3024
		Marsdenia	*Marsdenia longipedicellata*	BATT295-10	Ford 4794
		Melodinus	*Melodinus bacellianus*	BATT766-10	Ford 4298
		Neisosperma	*Neisosperma powerii*	A28	Costion 1365
		Parsonsia	*Parsonsia velutina*	C70	Costion 1606
		Secamone	*Secamone elliptica*	BATT825-10	Gray 8450

		Tabernaemontana	*Tabernaemontana pandacqui*	BATT211-10	Costion 2168
		Tylophora	*Tylophora williamsii*	BATT837-10	Ford 3713
		Wrightia	*Wrightia laevis*	CERF113-10	Ford 3794
	Gentianaceae	*Fagraea*	*Fagraea cambagei*	BATT647-10	Costion 2012
		Geniostoma	*Geniostoma rupestre var. australiana*	D19	Costion 1663
	Loganiaceae	*Mitrasacme*	*Mitrasacme oasena*	GenBank	DQ660653
		Strychnos	*Strychnos minor*	UH04	SAS 1788
	Rubiaceae	*Aidia*	*Aidia racemosa*	AA F04	Costion 3113
		Antirhea	*Antirhea sp. (Mt Lewis)*	BATT492-10	Sanderson K. 480
		Atractocarpus	*Atractocarpus hirtus*	BATT094-10	Costion 2113
		Bobea	*Bobea myrtoides*	BATT631-10	Costion 1972
		Canthium	*Canthium lamprophyllum*	A36	Costion 1373
		Coelospermum	*Coelospermum purpureum*	D72	Costion 1710
		Cyclophyllum	*Cyclophyllum multiflorum*	KB07	Ford 2119
		Gardenia	*Gardenia ovularis*	BATT120-10	Costion 2197
		Gen	*Gen Aq. 124851*	KA07	Ford 5406
		Gen	*Gen Aq520454*	BATT085-10	Cooper 1355
		Geophila	*Geophila repens*	BATT317-10	Ford 4521
		Guettarda	*Guettarda speciosa*	BATT274-10	Ford 5622
		Gynochthodes	*Gynochthodes oresbia*	LA07	Harrington LA07
		Hedyotis	*Hedyotis caerulea*	GenBank	AJ288604
		Ixora	*Ixora oreogena*	C45	Costion 1580
		Lasianthus	*Lasianthus kurzii*	G77	Costion 2013
		Morinda	*Morinda reticulata*	BATT773-10	Costion 2073
		Myrmecodia	*Myrmecodia sp.*	BATT271-10	Costion 2134
		Nauclea	*Nauclea orientalis*	E47	JC 843
		Neonauclea	*Neonauclea glabra*	BATT025-10	Costion 2220
		Ophiorrhiza	*Ophiorrhiza australiana*	H37	Costion 2069
		Pavetta	*Pavetta platyclada*	GenBank	AJ318451
		Psychotria	*Psychotria dallachiana*	C95	Costion 1633
		Psydrax	*Psydrax laxiflorens*	BATT745-10	Costion 1821
		Randia	*Randia tuberculosa*	B42	Costion 1468
		Tarenna	*Tarenna dallachiana*	BATT698-10	Costion 1645
		Timonius	*Timonius singularis*	CERF150-10	Crayn 1170
		Uncaria	*Uncaria cordata*	MA11	Ford 5613
		Wendlandia	*Wendlandia inclusa*	BATT224-10	Costion 2236
Lamiales	Acanthaceae	*Graptophyllum*	*Graptophyllum excelsum*	D1818	Harrington D1818
		Hypoestes	*Hypoestes floribunda*	BATT824-10	Gray 8055
		Pseuderanthemum	*Pseuderanthemum variabile*	BATT836-10	Gray 8399
		Ruellia	*Ruellia sp.*	BATT812-10	Ford 3647
		Thunbergia	*Thunbergia mysorensis*	GenBank	AY008828

	Bignoniaceae	*Deplanchea*	*Deplanchea tetraphylla*	BATT543-10	JC 10
		Pandorea	*Pandorea pandorana*	BATT634-10	Costion 1984
		Tecomanthe	*Tecomanthe sp. (Roaring Meg)*	CERF148-10	Zich 637
	Gesneriaceae	*Boea*	*Boea kinnearii*	BATT848-10	Gray 7986
		Crytandra	*Crytandra baileyi*	D44	Costion 1687
		Lenbrassia	*Lenbrassia australiana*	C53	Costion 1589
	Lamiaceae	*Basilicum*	*Basilicum polystachyon*	BATT352-10	Waterhouse 4961
		Callicarpa	*Callicarpa longifolia*	E64	Costion 1799
		Clerodendrum	*Clerodendrum floribundum var. ovatum*	F62	Costion 1900
		Faradaya	*Faradaya splendida*	BATT741-10	Costion 1804
		Glossocarya	*Glossocarya hemiderma*	BATT509-10	Costion 1610
		Gmelina	*Gmelina fasciculflora*	BATT449-10	Sanderson K. 945
		Orthosiphon	*Orthosiphon aristatus*	BATT765-10	Ford 4087
		Plectranthus	*Plectranthus amicorum*	BATT777-10	Gray 8165
		Premna	*Premna serratifolia*	BATT218-10	Costion 2138
		Vitex	*Vitex acuminata*	UA07	Costion 2756
		Viticipremna	*Viticipremna queenslandica*	BATT048-10	Costion 2201
	Oleaceae	*Chionanthus*	*Chionanthus axillaris*	BATT414-10	Sanderson K. 134
		Jasminum	*Jasminum simplicifolium*	BATT702-10	Costion 1659
		Ligustrum	*Ligustrum australianum*	D95	Gray 2396
		Olea	*Olea paniculata*	CERF652-11	Ford 2094
	Scrophulariaceae	*Myoporum*	*Myoporum montanum*	BATT309-10	Ford 4844
Solanales	Convolvulaceae	*Bonamia*	*Bonamia dietrichiana*	BATT340-10	Ford 3467
		Ericybe	*Ericybe coccinea*	BATT084-10	Costion 2206
		Ipomoea	*Ipomoea velutina*	BATT260-10	Costion 2212
		Lepistemon	*Lepistemon owariensis*	GenBank	AY100969
		Lepistemon	*Lepistemon urceolatus*	KH10	Hyland 16373
		Merremia	*Merremia peltata*	UA6	SAS 1900
	Solanaceae	*Lycianthes*	*Lycianthes shanesii*	BATT368-10	Ford 5248
		Physalis	*Physalis peruviana*	GenBank	FJ914181
		Solanum	*Solanum viridifolium*	BATT700-10	Costion 1643
Euasterids II					
Aquifoliales	Aquifoliaceae	*Ilex*	*Ilex sp. (Gadgarra)*	D50	Costion 1699
		Sphenostemon	*Sphenostemon lobosporus*	A54	Risley 348
	Cardiopteridaceae	*Cardiopteris*	*Cardiopteris quinqueloba*	GenBank	AJ402936
		Citronella	*Citronella smythii*	BATT445-10	Costion 1445
	Stemonuraceae	*Gomphandra*	*Gomphandra australiana*	WD11	Costion 3024

		Irvingbaileya	*Irvingbaileya australis*	BATT443-10	Costion 1443
Asterales	Alseuosmiaceae	*Crispiloba*	*Crispiloba disperma*	MB09	Costion 2238
	Argophyllaceae	*Argophyllum*	*Argophyllum cryptophlebium*	JD04	Harrington JD04
	Asteraceae	*Adenostemma*	*Adenostemma macrophyllum*	BATT292-10	Ford 1697
		Cyanthillium	*Cyanthillium cinereum**	BATT316-10	Gray 8106
		Eclipta	*Eclipta prostrata*	GenBank	GQ436456
		Helichrysum	*Helichrysum cymosum*	GenBank	AM234877
	Goodeniaceae	*Scaevola*	*Scaevola enantophylla*	CERF159-10	Cooper WW 2078
	Rousseaceae	*Abrophyllum*	*Abrophyllum ornans*	C32	Costion 1553
Escalloniales	Escalloniaceae	*Polyosma*	*Polyosma alangiacea*	BATT630-10	Costion 1975
Paracryphiales	Paracryphiaceae	*Quintinia*	*Quintinia quatrefagesii*	BATT273-10	SJD 1902
Apiales	Apiaceae	*Centella*	*Centella asiatica*	BATT157-10	Gray 8006
		Delarbrea	*Delarbrea michieana*	GenBank	GBU50243
		Hydrocotyle	*Hydrocotyle vulgaris*	GenBank	DQ133813
		Oenanthe	*Oenanthe javanica*	BATT854-10	Burchill AT 26
		Trachymene	*Trachymene coerulea*	GenBank	AY188437
	Araliaceae	*Cephalaralia*	*Cephalaralia cephalobotrys*	KD06	Ford 3246
		Mackinlaya	*Mackinlaya confusa*	BATT533-10	Costion 1682
		Motherwellia	*Motherwellia haplosciadea*	BATT343-10	Ford 5340
		Polyscias	*Polyscias australiana*	BATT401-10	Costion 1383
		Schefflera	*Schefflera bractescens*	E29	DOC 591
	Pennantiaceae	*Pennantia*	*Pennantia cunninghamii*	CERF168-10	Ford 4797
	Pittosproaceae	*Auranticarpa*	*Auranticarpa papyracea*	B38	Costion 1463
		Bursaria	*Bursaria incana*	PA08	Gray 7726
		Pittosporum	*Pittosporum rubiginosum*	BATT009-10	Costion 1669

Figure S1: Basal angiosperm tree from ML analysis.

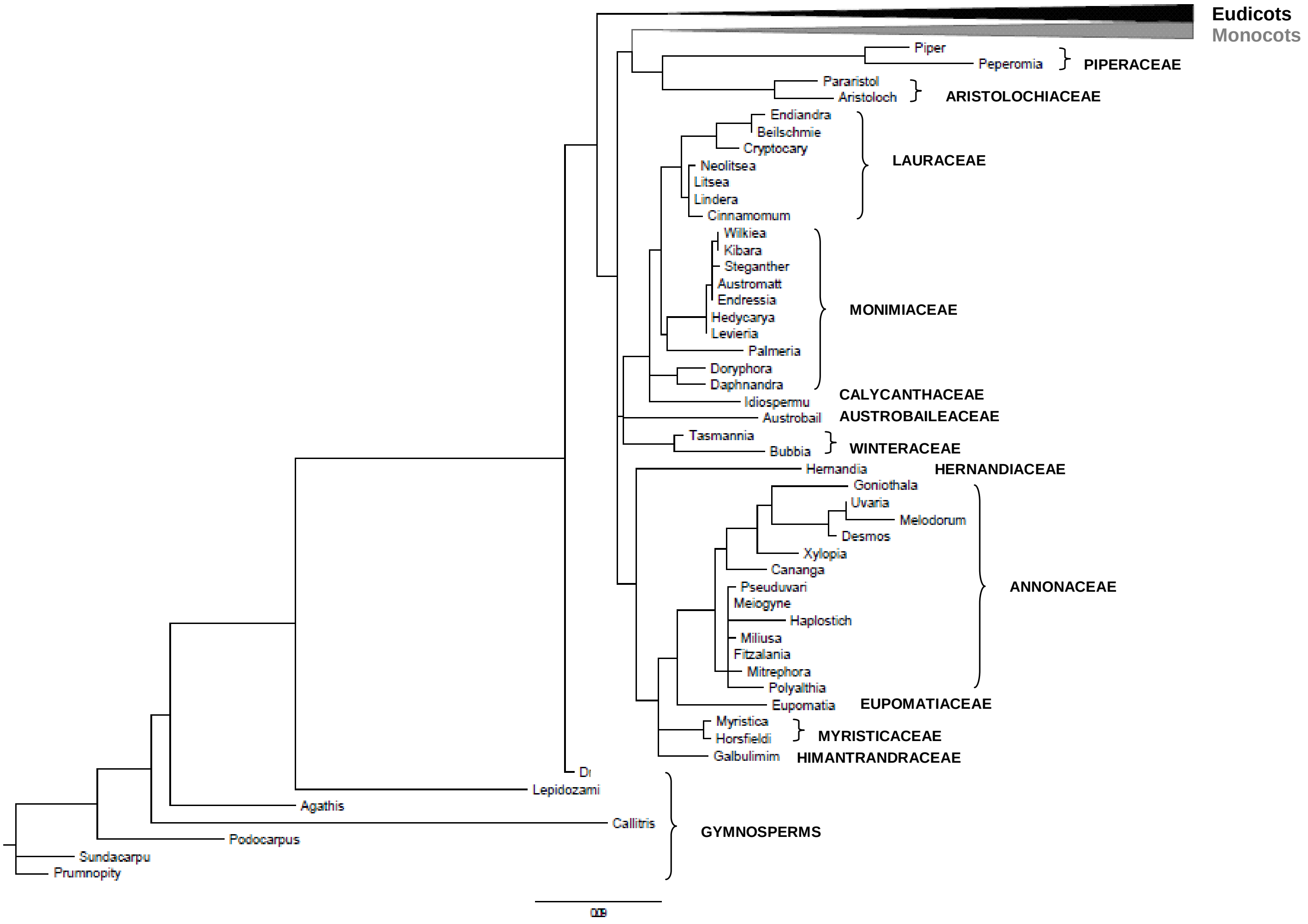


Figure S2: Monocot tree from ML analysis.

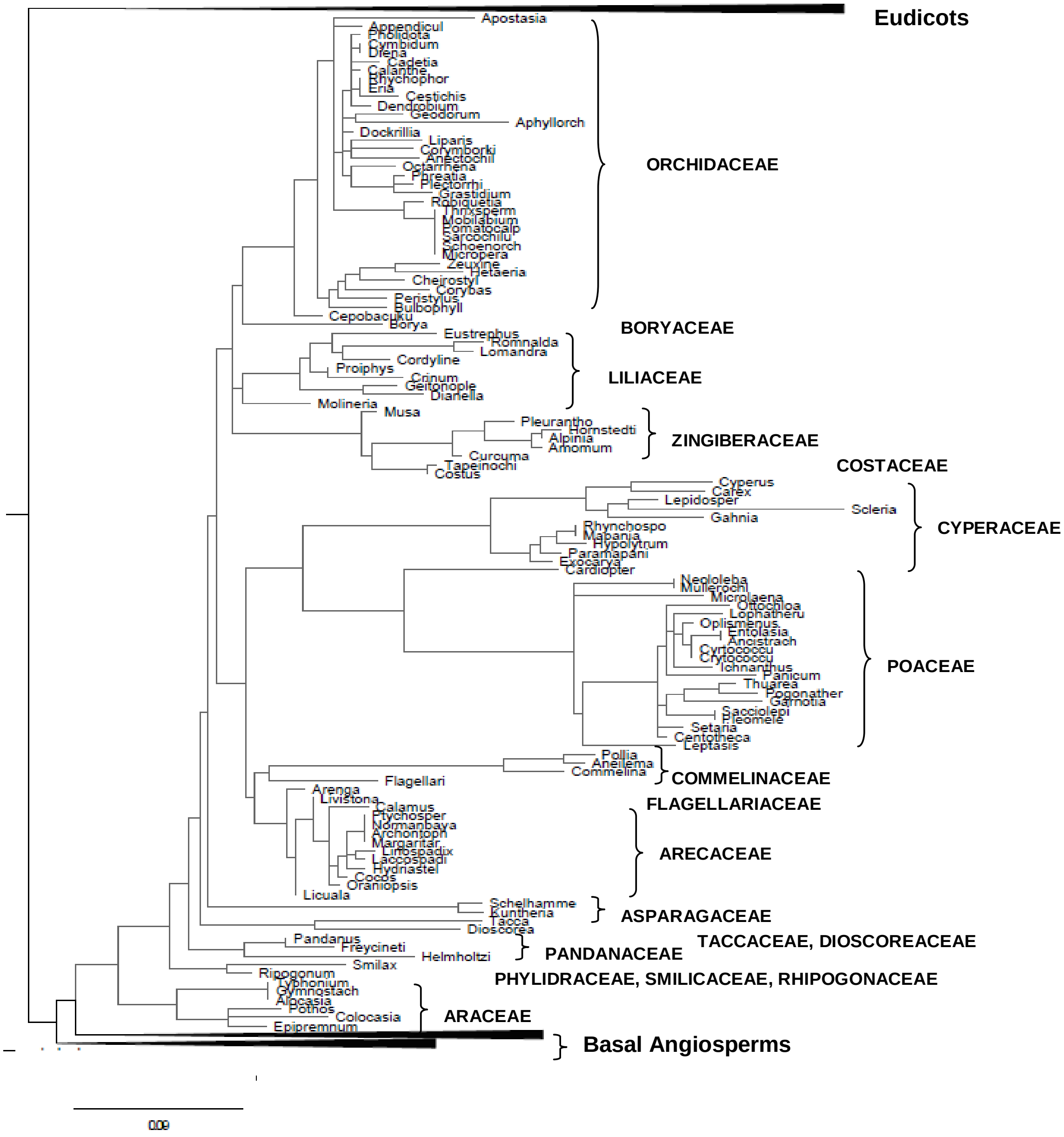


Figure S3: Basal and Core Eudicot tree from ML analysis.

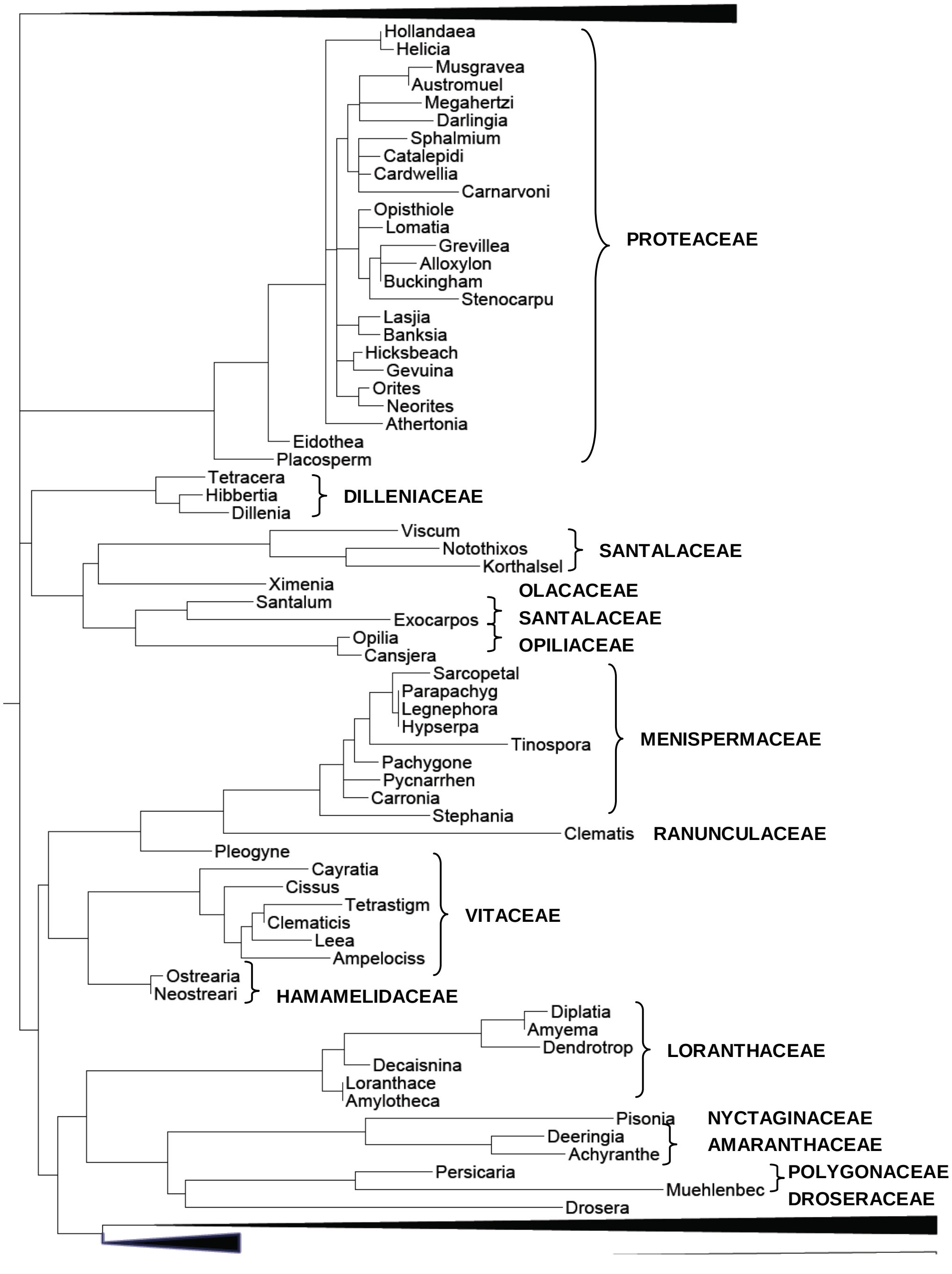


Figure S4: Eurosids I tree (part I) from ML analysis (continued in Figure S5)

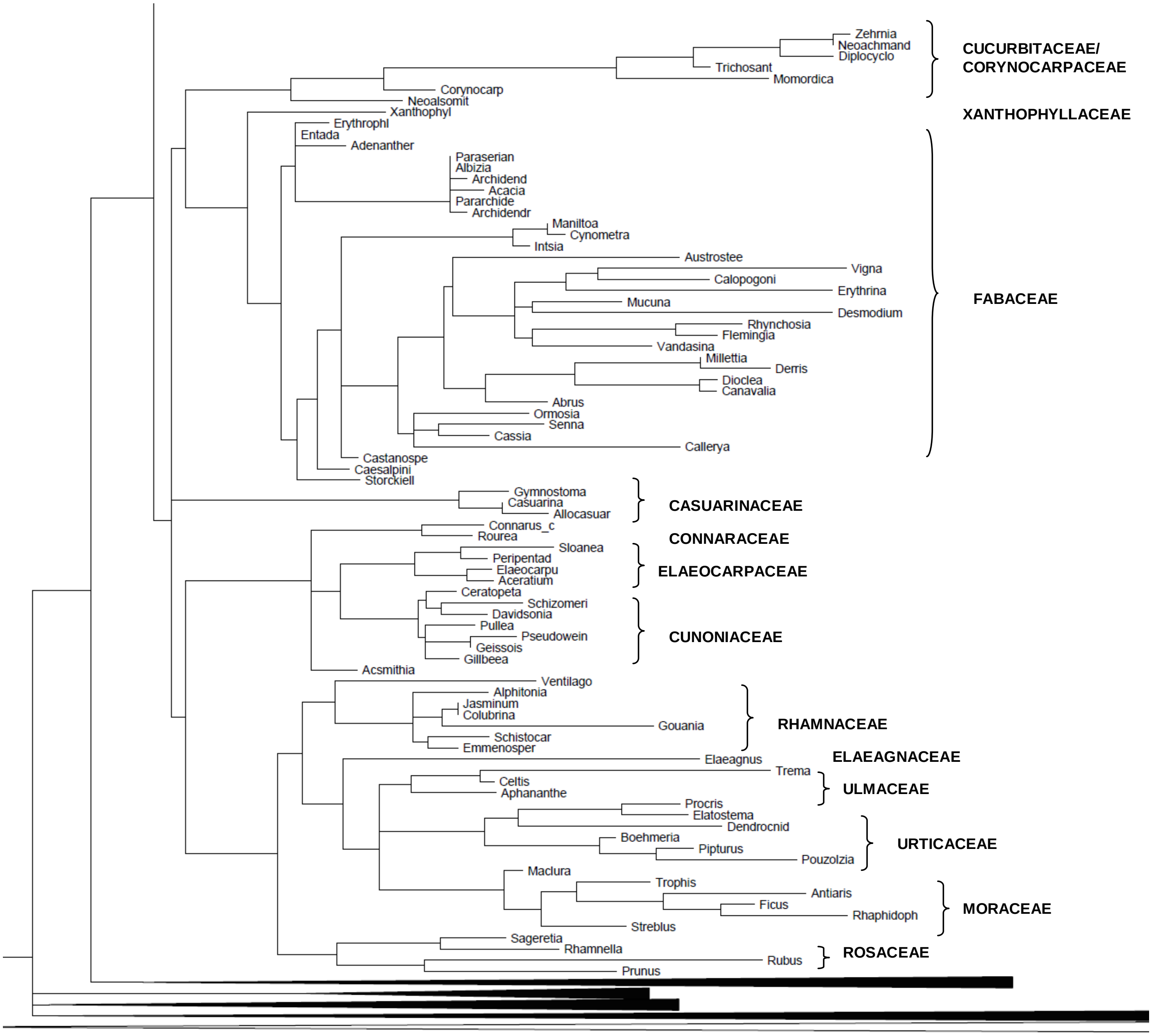


Figure S5: Eurosids I tree (part 2) from ML analysis (continued from Figure S4).

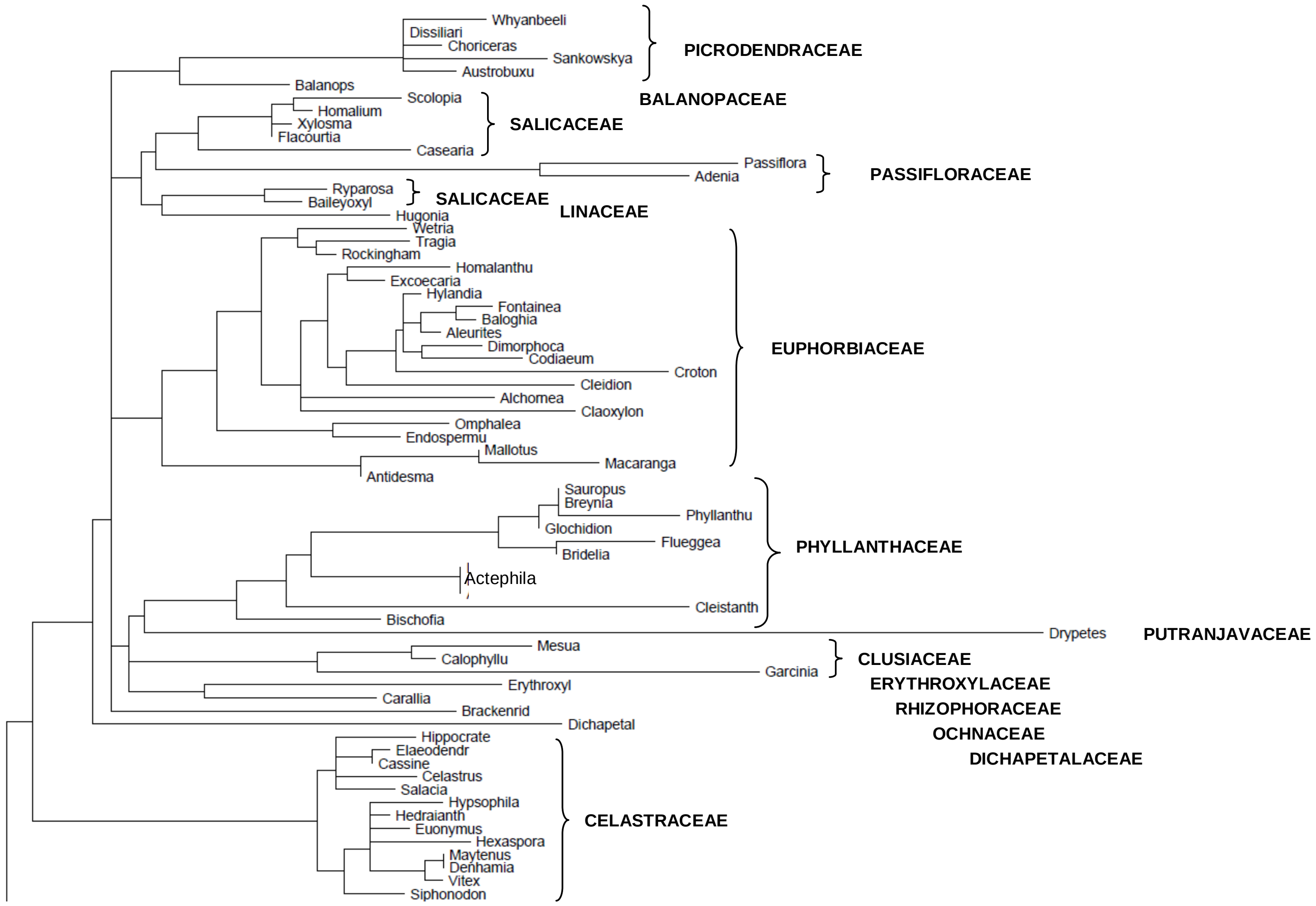


Figure S6: Eurosids II tree (part 1) from ML analysis.

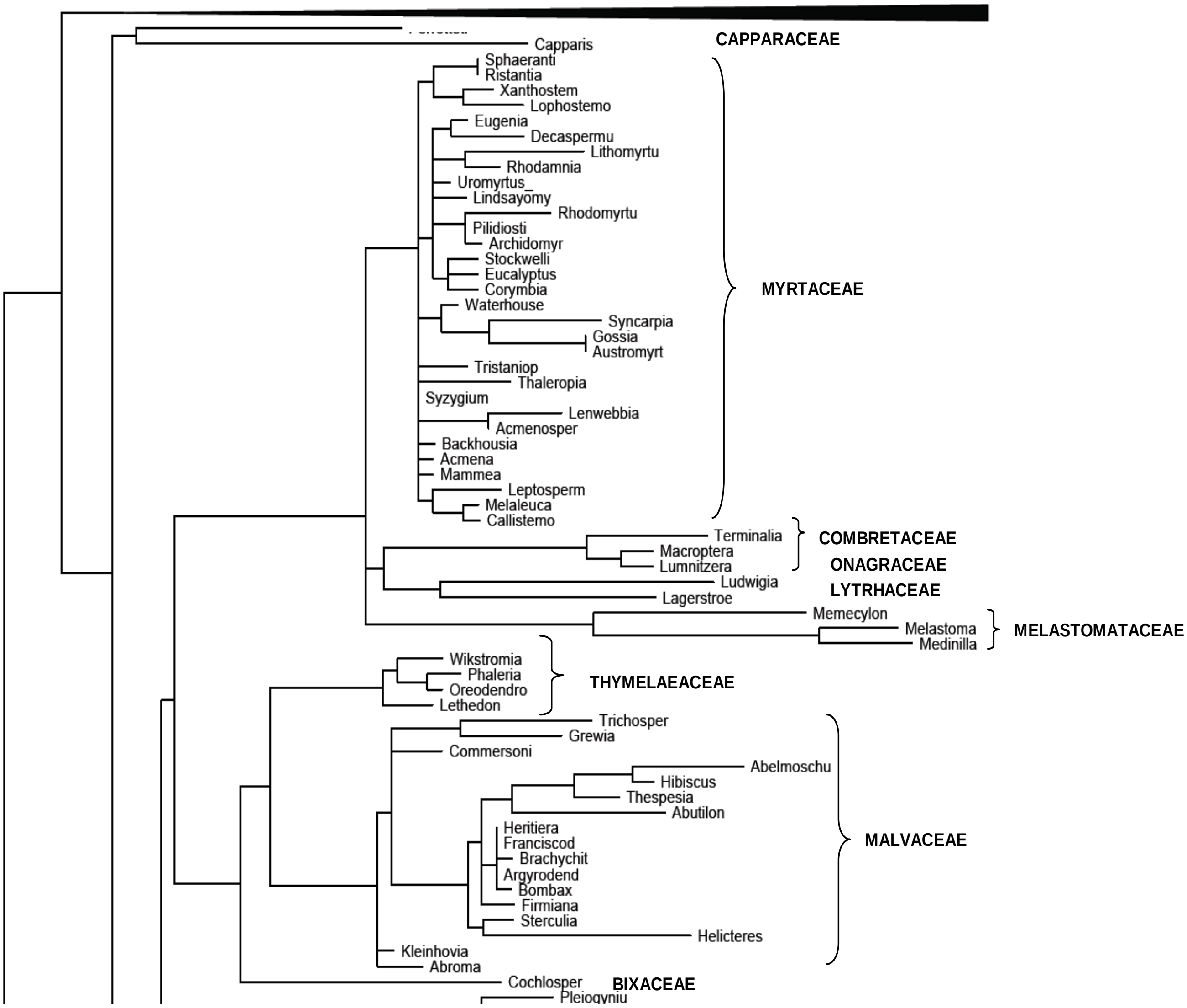


Figure S7: Eurosids II tree (part two) from ML analysis

Figure S8: Euasterids I tree (part 1) from ML analysis.

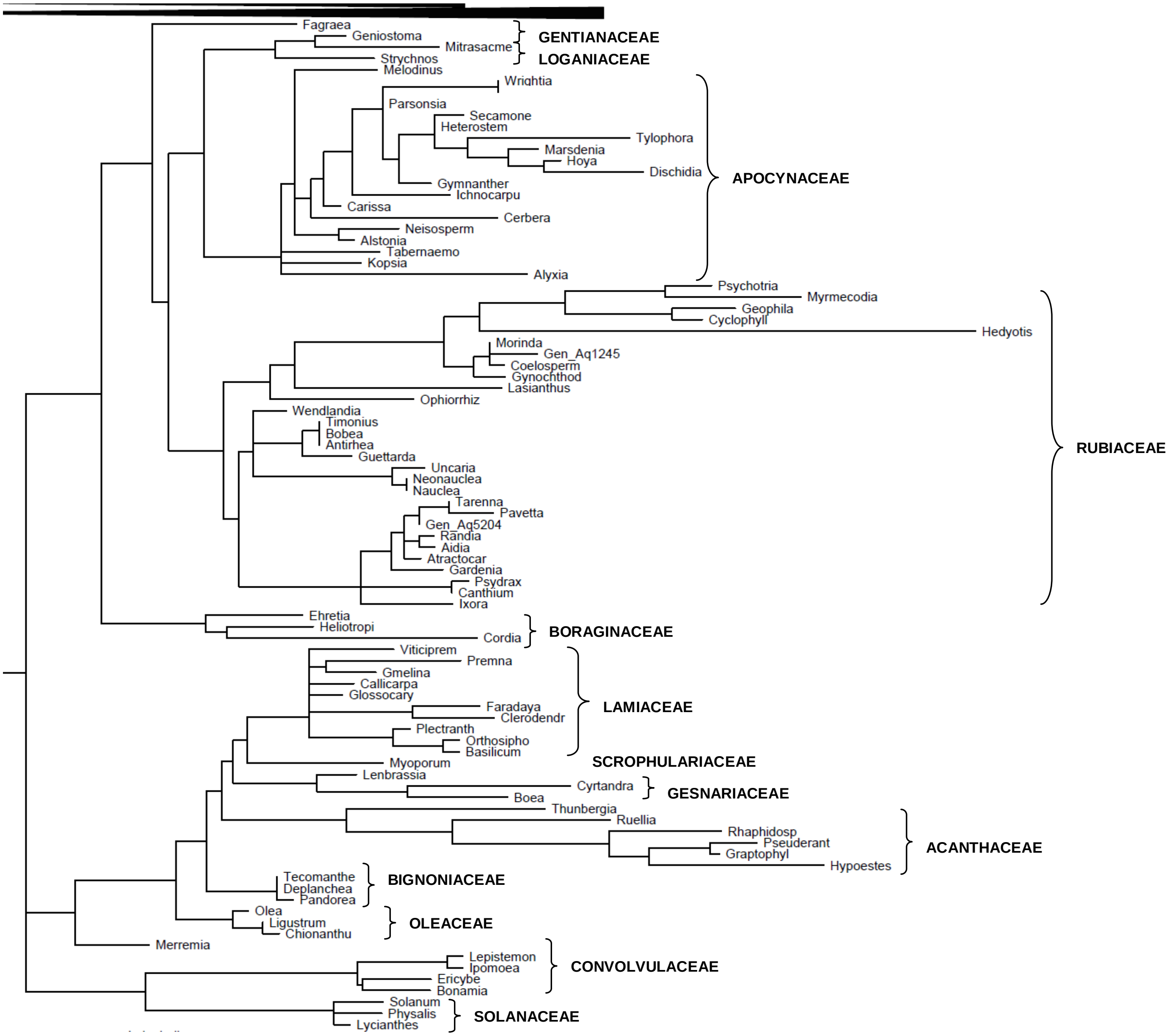


Figure S9: Euasterids I tree (part 2) from ML analysis.

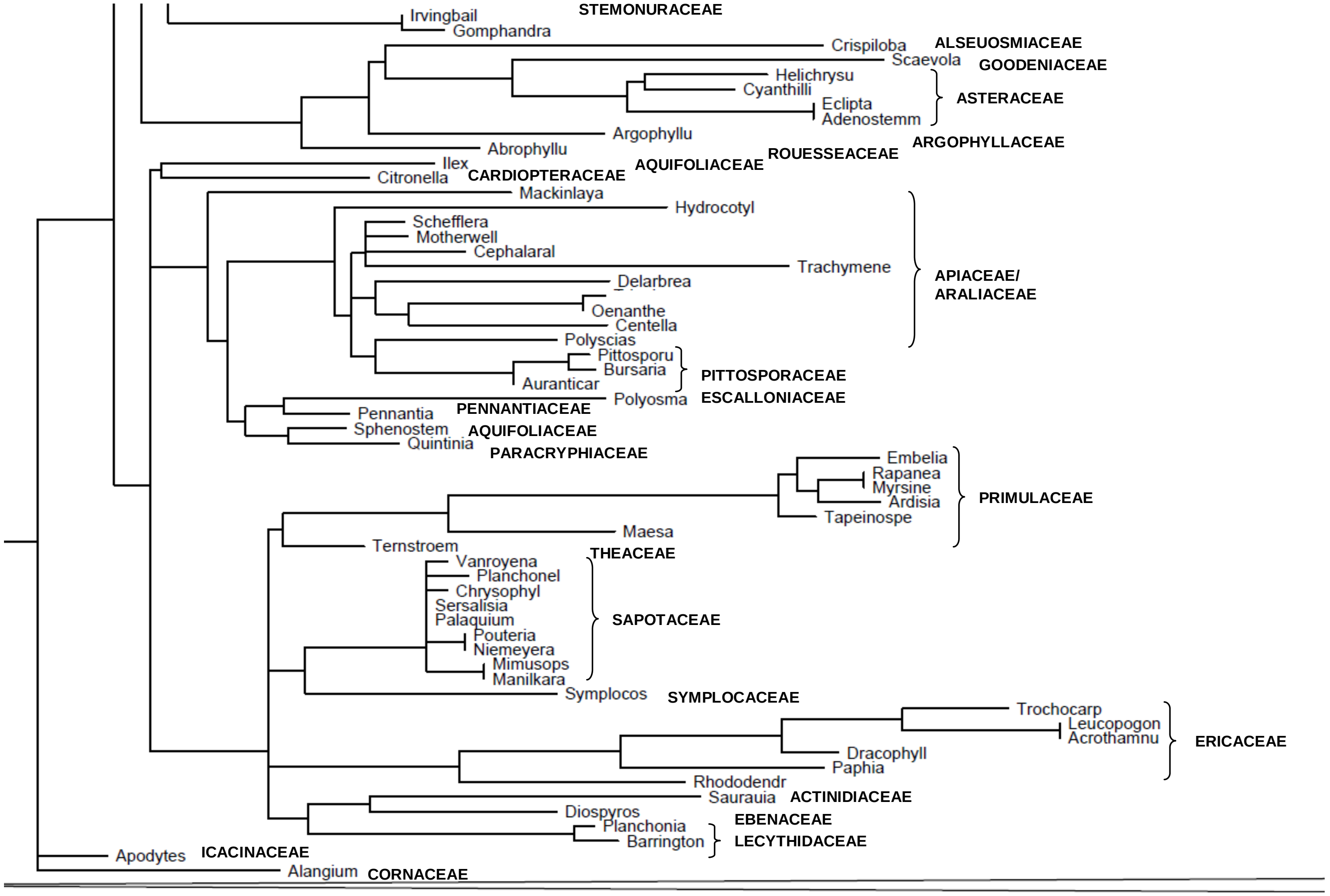
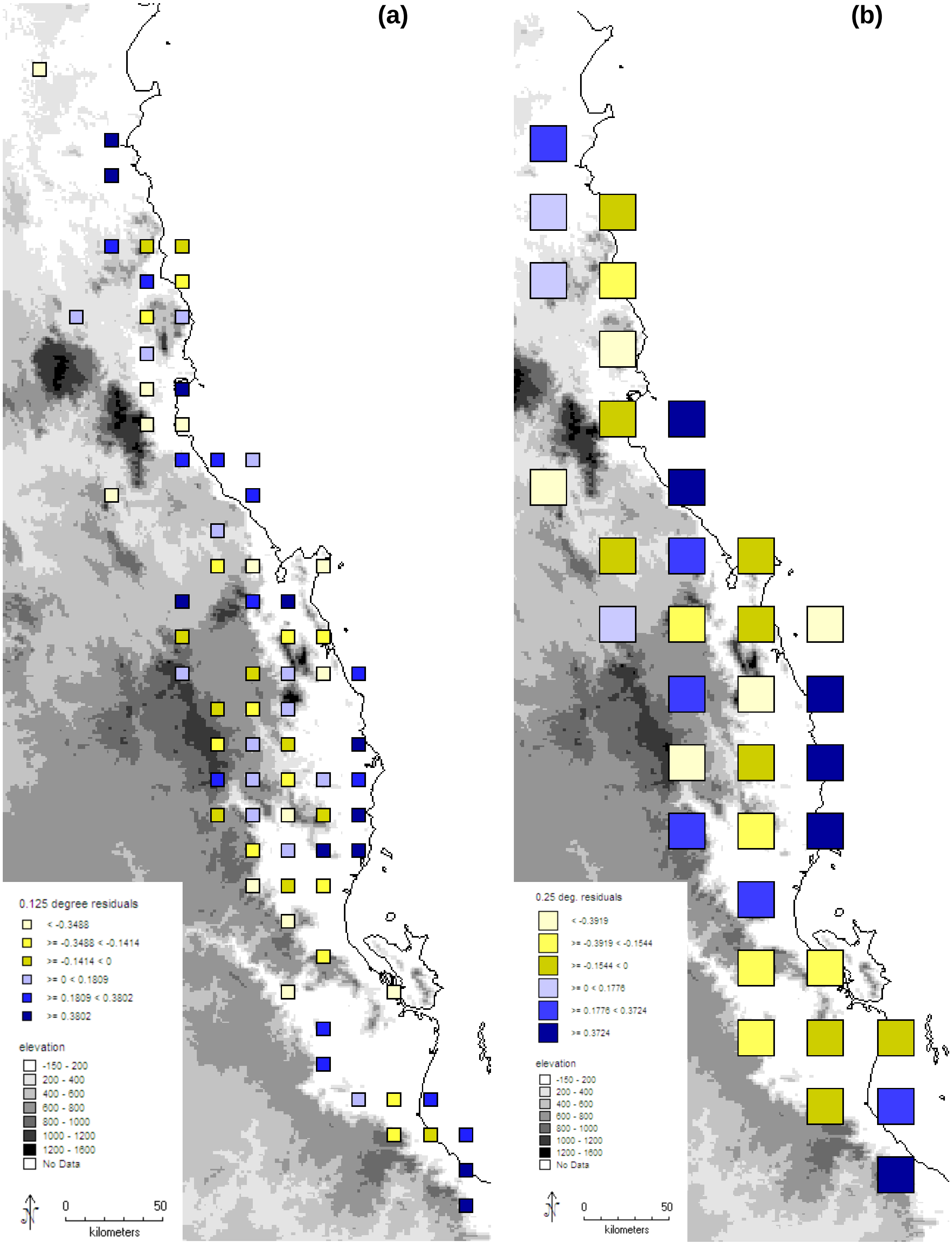


Figure S10: Negative residuals (yellow) and positive residuals (blue) at 0.125° scale (a) and 0.25° scale (b)



THESIS CONCLUSIONS

This thesis has advanced biodiversity knowledge at a regional scale in three separate bioregions, each of which had different levels of existing knowledge prior to this project. In the region of Micronesia, which comprises approximately one third of the Pacific bioregion, a complete list of endemic plant species was absent until now. It is argued that this is a critical first step in assessing the biodiversity value of a particular region. Although the subjective nature of taxonomy in general renders it a questionable scientific discipline to some, it is undeniable that alpha taxonomy and checklist compilations such as those presented in Chapters 1 and 3, lay a foundation for addressing a myriad of other biodiversity and conservation related questions that are essential to the life sciences.

When species concepts on oceanic islands are resolved, immediately one has access to scientifically supported data on the extent of occurrence or total distribution of the species that occur there. In the case of Palau, this baseline data was utilized to attempt IUCN assessment of all the endemic plant species. Our study demonstrated that there was insufficient data for meeting IUCN red list criteria. Instead of succumbing to this limitation we used our example from Palau to highlight the hard realities of relying on a one size fits all solution to the problem of assessing extinction threat to species. By reviewing the most up to date literature on plant species counts for the major archipelagos of the Pacific, we found that only 3% of the native plant species in the Pacific Islands region have been assessed with IUCN red list criteria.

Considering that the Convention on Biological Diversity’s (CBD) Global Strategy for Plant Conservation (GSPC) aims to assess the threatened status of all known plant species of the world by 2020, at least one thing is clear. Alternative methods of establishing threatened status of species must be widely acknowledged and given equal or comparable accreditation to the IUCN red list. Anyone who advocates that the GSPC target must be achieved solely through utilizing the IUCN Criteria clearly does not understand the size and complexity of task at hand. In the case of Micronesia, I demonstrate that a high percentage of plant species are either very rare or known from only a few scientific collections. Many of these species occur in areas that are difficult to access and are unlikely to be surveyed for the type of population level data that is required to meet IUCN Criteria. It is argued that especially in cases such as these, where species are known to have a very restricted distribution, such as single island endemics, alternative threatened assessment criteria are required.

In Chapter 2 we presented one such alternative methodology by enabling the use of historic and archaeological evidence of landscape change and disturbance. Deforestation is often viewed as primarily a modern problem, however ample data exists from habitats around the world to support pre-historic human activities that have lead to large-scale deforestation and environmental decline. Most current conservation policy and threat assessment schemes however only consider recent declines in habitat or species. This may very well be logical in “cold spot” bioregions such as temperate North America where many parts of the eastern deciduous forests have re-covered from nearly complete deforestation. This logic however must be used with caution in the tropics and especially in biodiversity “hot spots” where species are known to have very restricted distribution or be exceptionally vulnerable to invasive species, such as on oceanic islands. Some invertebrate biotas of the Pacific islands are known to have undergone nearly complete species compositional turnover with both the arrival of early humans and again with the arrival of European colonists. Many seemingly “natural” habitats of the world may indeed be proven to be impoverished ecosystems as a direct consequence of early human activity. Certainly, many already have been proven to be so.

Using an interdisciplinary approach in Chapter 2, one such habitat, the savanna vegetation of Palau, is proven to have an anthropogenic origin. Although traditionally such questions are left to the business of archeologists and historians of primarily academic orientation, we argue that the outcomes of resolving such a question have far reaching consequences and impacts. In the case of Palau, it enabled quantification of a minimum extent of historic deforestation thereby enabling total decline in habitat for the majority of the island’s endemic plant species. This type of information is not just useful for academic thought, it is pertinent to current conservation schemes and policies. A patch of forest may have remained stable over the past 100 years, but if it is the last remaining patch of a forest that once stretched across an area 95 times the size of the extant area prior to human habitation, then any species endemic to that particular forest habitat has undergone a 95% decline in its original distribution range. This hypothetical example may be extreme, but it is relevant to the real biodiversity concerns in hotspot and tropical bioregions. Species in such conditions may actually be on the brink of extinction, but not qualify for threatened status under the IUCN Criteria. This raises question to the accuracy of term “Vulnerable” applied under the IUCN system. Does the IUCN category “Vulnerable” accurately reflect the actual vulnerability of species of tropical plants or other taxonomic groups on small oceanic islands and other poorly known tropical regions?

In Chapter 3, our arguments highlighted in the previous chapters are taken further by bringing a global perspective to the importance of the endemic plants of Micronesia. Chapter 3 also simultaneously serves to provide a baseline resource for people working within the bioregion that can make relevant decisions and act locally. Thus the manuscript addresses the interests of both the scientific community and people working in applied conservation. The gap between scientific research and conservation on ground is a widely accepted problem. I attempt to address this problem by providing a scientifically supported product that presents the relevant and necessary information in both a widely accessible and engaging format. To date, all information on the endemic status of plant species in Micronesia has been buried in technical taxonomic papers, which are jargon filled, sometimes completely in Latin, and published in scattered academic journals, often obscure and sometimes even difficult to access from top botanical institutions.

The checklist of Micronesia’s endemic plant species is published in *Micronesica*, an open access, online, peer reviewed journal. This will ensure not only ease of access, but permanence of the data presented as many of the relevant literature on Micronesia’s flora are now out of print. Since few native Micronesians have the opportunity to enroll in higher education, I felt that the paper should not be entirely technical in nature but also provide information about the respective taxa in common English. This may have detracted from the paper's scientific rigor but the value of potentially engaging and captivating the interests of the native Micronesians, the people with the direct power to ensure preservation of their biodiversity, was considered a valuable trade off. The paper does however simultaneously and appropriately address a question of high scientific profile; global hotspots of biodiversity.

By comparing data on the number of endemics per island in Micronesia to other Pacific archipelagos and recognized biodiversity hotspots around the world, it is shown that Micronesia has the highest percent of plant endemism, calculated by number of endemics per square kilometer, out of all globally recognized biodiversity hotspots. This is despite the fact that historically, the geographic consequence of the size of the islands of Micronesia has for the most part rendered them a forgotten and under-valued bioregion. Perhaps the most emotionally gripping example is the development of the atomic bomb, for which the majority of nuclear testing took place in Micronesia. The islands that were systematically vaporized during the nuclear testing included some of the oldest geological atoll island formations on earth and lead to the displacement of entire populations of people in the Marshall Islands. The sheer size of the islands and the numbers of displaced people statistically however, may have been considered small and insignificant enough to justify the decision. Similarly 350 endemic plant species (the total for Micronesia) does not sound like very much and could be easily ignored or considered insignificant, however the percent of endemism observed in Micronesia clearly emphasizes the power of the telescoping effect on islands and that sheer numbers must be viewed in context.

Oceanic islands are like condensed versions of continental regions. They may be small in terms of total land area, but this total area often represents more biodiversity then continental areas of similar size. Altitudinal zoning is shrunk (the telescoping effect), which explains why the island of Pohnpei in Micronesia is home to the lowest elevation cloud forest on earth, and species that ordinarily would occupy much larger ranges specialize and diversify into unique taxa that occupy only a very small area or unique habitat. Reiterating directly from the manuscript's conclusion, "the tiny islands of Micronesia may be small geographically, however, their importance to the world in maintaining reserves of unique biodiversity is not small by any means," the story of Micronesia is one of size and scale. It is hoped that a longer-term outcome of this study will be the enhanced appreciation for the hugeness of biodiversity and natural history that can be found in small areas such as Micronesia and that this depth of context may increase the global value attributed to them regardless of their geographic size.

Perhaps the most significant lesson to be inferred from this study is the fact that such a large portion of the globe is lacking such an essential baseline source of data. As the field of biology propels itself into the molecular age, it must not be forgotten that many parts of the world are in need of more basic progress in alpha taxonomy. The production of this work has virtually no financial costs involved aside from time. Biologists in developing nations can do a great service to parts of the world by sacrificing a small portion of their time to advancing or synthesizing knowledge in poorly described areas. These types of publications may not yield an immediate return or receive high citation rates, essential for career development, but they can form the foundation for such works and thus may bring a greater long-term return.

In Chapter 4 we tested whether or not it was possible to go to such an area in the tropics where baseline data is lacking and accurately estimate the total number of species present using DNA barcodes. Many of the most species rich areas in the tropics are lacking this baseline data, or are at least difficult to conduct surveys in due to the need for fertile specimens or access to high forest canopies. Collecting fertile material from a tropical forest canopy is not a trivial undertaking, however rapid collection of DNA tissue can be achieved with a comparably minimal effort. Here is where a great potential lies in synchronizing the current drives of biological research focused on molecular evolution and traditional biodiversity discovery and documentation. Although DNA barcoding for vascular plants has proven problematic for distinguishing species that are closely related, I demonstrate that this method can provide an accurate estimate of the total species richness for an area. Such studies can simultaneously advance molecular knowledge by contributing to GenBank and the BOLD barcode of life database and serve as a first step towards full fledged taxonomy by grouping individuals into hypothetical species. DNA barcoding has the potential to revitalize and increase the value attributed to alpha taxonomy and bio-discovery research and has already begun to do so.

Although the present technology for generating DNA sequence data may make a DNA sample based biodiversity inventory restrictive in some regions, it is expected that both the financial expense and technological efficiency will improve substantially over the next decade. It is envisioned that this will make biodiversity and biological research more accessible to people without specialist expertise but more importantly vastly increase the amount of data collection and improve accessibility with web-based platforms. Verifying the identity of a biological specimen requires taxonomic expertise, which is a rare and declining skill, but anyone can collect a DNA specimen. These collections can funnel into the barcode of life database. Once the species are verified, then collection records can be multiplied ten fold if DNA barcode based biodiversity inventory applications make headway in poorly inventoried regions. This holds a great promise for tropical regions, such as those showcased in the former chapters of this thesis. When species barcodes are obtained and resolved in such regions, progress towards obtaining a better understanding of the extent of occurrence or natural distribution of species is likely to accelerate.

In Part 2 of this thesis, I use two case studies from comparatively well-sampled bioregions to give an insight into the breadth of scope and complexity of the current biodiversity crisis. Chapter 5 presents in a way, a biologist’s worst dream, come true. In all the preceding chapters the lack of available data to inform conservation prioritization is substantially emphasized. This would in a sense build up the impression that if the data were available then obviously it would be utilized to inform conservation policy. Chapter 5 represents a real world example where one of the most comprehensive biological survey datasets in the world is not used to prioritize and guide the planning of a major state initiative to identify biodiversity corridors. If that were not enough, instead of integrating the outcomes of this study and updating the plan accordingly, the recommendations to the state that came as a consequence of the results presented in Chapter 5 were for the most part completely ignored.

Our report found major inconsistencies with the goals of South Australia’s NatureLinks initiative and the actual plan on the ground in the East Meets West region. Although the initiative claims that minimizing species loss and mitigating the affects of fragmented populations are part of the primary aims, this is not fully supported by the results presented in our study. This chapter serves to provide a case study of the sobering realities of conservation in practice. The biologist will always yearn for a better and optimal dataset with its application to conservation outcomes as a characteristic rally call. However, this chapter serves as an example that good data does not by default lead to good conservation outcomes. Conservation outcomes are achieved when strong links between science, policy, and economics are established and balanced. At times this will require utilizing the best data available. Certainly when the high-resolution data is available it should be expected to be utilized as a resource for guiding policy. The types of analyses presented in Chapter 5 are standard and basic biodiversity indices that have proven useful for conservation prioritization around the world. More robust and improved indices and modeling procedures are constantly in development and authoring a new approach to analyzing biodiversity data is held in high respect in the academic community. Continual improvement is of course commended, however it is cautioned that in this quest, the primary purpose of these methods is not forgotten.

If state governments will not even utilize standard biodiversity indices for guiding conservation schemes perhaps more time and energy should be spent in building stronger links between science and policy. New journals are emerging that encourage the publication of conservation success stories. These journals provide opportunities for scientists to pursue this avenue while maintaining their publication quotas. New methods are of course commended and desired, just not at the expense of their end goal. This will require some unorthodox use of time from many scientists and academics around the world but it is evident that simply publishing scientific studies in peer-reviewed journals is not enough to achieve on ground conservation success. Strong links between science and policy are essential and must be encouraged by the institutions that employ people of these respective disciplines.

Chapter 6 presents an altogether different scenario. In the Queensland Wet Tropics, I analyzed a comprehensive dataset that spanned a bioregion mostly protected by existing reserves (with the exception of some habitat types). The accessibility of the Wet Tropics of Queensland has rendered them an optimal tropical forest biome for exploring new methods in biology. My study focused on phylogenetic diversity (PD), which as a method is now gaining popularity and support for use in conservation planning. The primary message of PD theory is that using species or other taxonomic units to estimate the biodiversity value of a region may be misleading because of the variance in diversification rates among species. Under the principles of PD, conserving three distantly related species is assigned higher value than conserving three closely related species. This primary message is logical but when translated onto a large dataset across an entire biome or landscape, the intuitive interpretation is that PD and taxonomic richness are not correlated thus taxonomic richness alone should not be used as the unit of measure in conservation prioritization schemes. This inference may however be misleading. In my study, overwhelming statistical support is found for a linear correlation between PD and taxonomic richness in the Queensland Wet Tropics. The lack of correlation between PD and taxonomic richness that has been documented in previous studies is in regards to complementarity of sites. This may be useful in conservation planning but does not devalue the role of using taxa as a unit of measure. The linear correlation between PD and taxonomic richness strongly suggests that traditional biodiversity estimates on which many conservation priorities are based are still valid and should be utilized where obtaining genomic data for large numbers of species is impractical.

What is interesting and useful about PD, is what it can tell you about a biome when the effects of taxonomic richness for interpreting the observed PD are removed from the data. This is done simply through a regression and then spatially mapping the positive and negative residual values. In the case of the Wet Tropics, this uncovered a remarkable biogeographic story, one that was of particular interest to Charles Darwin's closest supporter, Joseph Hooker. Joseph Hooker's travels in the South Seas included expeditions to Australia, which led to the publication of a significant paper on the phytogeography of northeast Queensland. Hooker was the first to describe the different components of this flora, including an Indomalayan element, an endemic Australian element, and a southern Gondwanan element.

These notions were later supported by Nancy Burbidge's famous doctoral dissertation but not long afterwards came under close scrutiny by a number of other highly esteemed botanists. These latter botanists formed an alternative school of thought advocating the Wet Tropics as an entirely Gondwanan or Australian derived flora. These sentiments have remained in the literature until very recently with the gradual publication of molecular phylogenies proving the incursion of particular lineages into the region from Southeast Asia. The present study however, provides for the first time a well-supported biome level dataset that not only statically proves the existence of this "Indomalayan" or "Sundanian" component, but also identifies its primary location in the landscape. A statistical correlation is found between areas with a high proportion of Sundanian taxa and low elevations. This result supports the intuitive inferences of numerous botanists who have observed and commented on the Gondwanan character of the uplands in Queensland and New Guinea. The known history of rainforest expansion and contraction in the region also seem to support this notion and the correlation between these lowland areas and higher PD values than expected based on the number of taxa is perfectly logical. One would expect to find a higher PD in locations that contain a higher proportion of distantly related lineages that have dispersed into Australia from other continents.

Chapter 6 shows that PD can provide insights of great depth and scope for the evolutionary history of an entire bioregion. When obtaining this level of molecular data is feasible, conservation biologists can then have at their fingertips a diverse array of analytical methods to approach reserve or park boundary justification, where different epochs of evolutionary history can be represented in the landscape. The Queensland Wet Tropics World Heritage area was established under the premise that it represented a diverse array of eras of evolutionary history, however distinguishing the location of these areas across the landscape was never attempted. This new enhanced level of data can now be utilized to re-assess how well the World Heritage boundaries represent these different evolutionary or floristic components. It is already well established that the lowlands of tropical north Queensland are the least well-represented habitat in the reserve system. The results of the present study strongly indicate that these lowland forests may be likened to that of a convergence or speciation zone being the primary cradle for a diverse array of lineages that have dispersed to Australia in the last few million years, then subsequently diversified into new species. Increasing representation of lowland rainforest in the Queensland Wet Tropics reserve network can now be supported with a substantial scientific underpinning.

This thesis has traversed several realms of thought in the disciplines of botany and evolutionary biology by drawing upon data from several exceptionally different and unique biological realms. In doing so, it is hoped that an accurate picture is painted of both the vastness of biodiversity on this planet and how little we really know about it. More importantly, that the different levels of existing knowledge in different bioregions may not necessarily be fundamentally important in determining how well conserved they are. It is alluded to that there is great potential that lies in synthesizing the directions of the molecular era with traditional bio-discovery and that as this is achieved there will likely be acceleration in availability of species level data. It is hoped that above all, progress made towards this end will be used to help conserve and manage biodiversity sustainably and that priority will be made to establish any necessary linkages between the disciplines of science, policy, and commerce to see that this is done. For biodiversity knowledge and awareness to evolve away from being the business of specialists to becoming a paradigm, this alone is the most important task.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the support of many people and institutions. I would like to especially thank the University of Adelaide for providing an international post-graduate scholarship, the Department of Environment and Natural Resources of South Australia for helping fund the PhD stipend, the Australian Tropical Herbarium for hosting me for the majority of my time, all my supervisors especially Andy Lowe and Darren Crayn for providing substantial financial contributions to the molecular work, CSIRO and especially Andrew Ford and Dan Metcalfe for data and collecting contributions, the Australian Commonwealth for funding my work in DNA barcoding, James Cook University for employing me part-time, all additional co-authors from the preceding chapters who made scientific contributions; Ann Kitalong, Tarita Holm, Jolie Liston, Akiko Ida, David Lorence, Hugh Cross, Mark Harrington, Jeff Foulkes, Peter Lang, Robert Brandle, Will Edwards, and James Richardson, all my colleagues at both the University of Adelaide and James Cook University and from the other side of the world, my family for supporting me along the way, my friends Fiona House and Tim Rogers for welcoming me and helping me settle in Australia, the Cairns salsa community, and all those un-named who contributed indirectly in any way.