

Research Article

## Forest structure, plant diversity and local endemism in a highly varied New Guinea landscape

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### Abstract

The Island of New Guinea is renowned for its high biodiversity, which arises in part from its complex geology and topographical variability. The island is, however, relatively understudied. We surveyed forest plant communities in the poorly studied Naoro-Brown catchment of the West Koiari region of Papua New Guinea. We identified four forest types—riverine successional forest, lower montane forest, hill forest, and riverine mixed forest—along a 13-km transect, and examined forest structure (tree height, stand density, and biomass) and tree species diversity (species richness, Shannon-Wiener diversity index, and composition) in these forest types. We also assessed the effect of local topography on floristic patterns. Forest structure and species diversity varied greatly among the forest types, with topography strongly affecting species assemblages. These results suggest that highly varied landscapes may contain high *beta* diversity via intense segregation and establishment of varied vegetation communities. *Beta* diversity in New Guinea may be higher than expected as such highly varied landscapes are common, yet poorly studied. To effectively conserve biodiversity in New Guinea's forests, protection must include forested landscapes that best represent the topographical variability throughout the island to account for locally endemic species restricted to specific ecological niches.

**Key words:** *Beta* diversity, Biodiversity conservation, Forest structure, Local endemism, Species diversity, Topographic variation.

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## Introduction

The island of New Guinea is estimated to contain 5-7% of total global biodiversity, making it one of the richest tropical biomes in the world [1-2]. There are at least two likely explanations for this. First, because of its geographic location, New Guinea is the confluence point for biodiversity from both Australasia and Southeast Asia [3]. Second, high habitat heterogeneity generated by the geological processes (tectonic uplift and volcanism) from which the island originated, have also enhanced diversity [4]. A classic example of this is the exceptionally high biodiversity found on Mount Bosavi, an extinct Pleistocene volcano in the Southern Highlands of Papua New Guinea [5]. In this area, topographical barriers have restricted species migration, promoting a radiation of new plant and animal species, many of which are locally endemic [5].

Much of the biodiversity in New Guinea is still undescribed scientifically, as evidenced by continued discoveries of new species in remote areas [e.g. 5-8]. Furthermore, information on species occurrences and the structural dynamics of biodiversity in multiple forest types is still far from adequate [9]. The only known published studies of the structural dynamics of biodiversity in New Guinea focused on insect herbivory and trophic interactions between food webs [e.g. 10-12]. In addition, recent publications provide novel information on diversity patterns of forest succession in New Guinea lowland forests [e.g. 57, 58]. Despite the biological advances in New Guinea, information on the diversity and composition of plant communities is still scarce.

Previous plant surveys in New Guinea mainly focused on *alpha* diversity, which is the species richness within a localised area [13-14]. These surveys reported tree richness ranging from 98 to 178 species per hectare [e.g. 15-19], with the highest published estimate of tree and liana diversity ( $\geq 10$ cm diameter-at-breast height [DBH]) reaching 228 species per hectare in the Crater Mountain Wildlife Management Area [16]. However, *beta* diversity, the variation in species composition through space [13-14], remains virtually unstudied in New Guinea. Understanding patterns of *beta* diversity is crucial for guiding conservation efforts in rich tropical biomes such as New Guinea that are being rapidly altered by deforestation and forest degradation [2, 14].

The relative lack of biodiversity surveys in New Guinea have been attributed to financial constraints, limited availability of experts, and the difficulty of accessing many areas due to highly rugged terrain [18, 20-22]. However, increasing human encroachment into old-growth forests is leading to increasing numbers of environmental impact assessments, which often involve rapid plant surveys. Such surveys could improve the spatial resolution of plant compositional data and thereby allow *beta* diversity to be better estimated in New Guinea [e.g. 23].

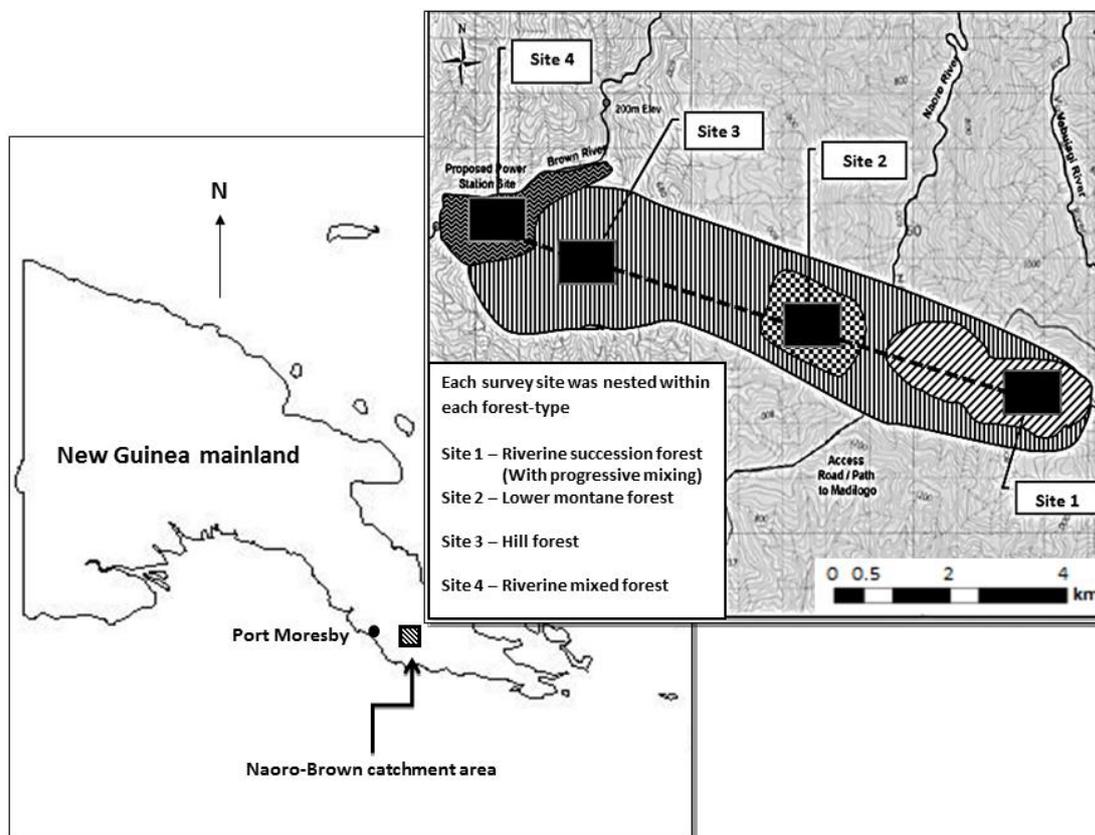
Here we present a study of forest structure and floristics in a rugged New Guinea landscape from such a rapid plant survey. Specifically, we ask: (1) Do forest types within the Naoro-Brown River catchment vary considerably in structure and plant richness? (2) How does *beta* diversity vary among the major forest types? (3) Does local topography influence plant endemism within this catchment?

## Methods

### *Study Location*

Our study was conducted in July 2010 along a 13-km transect within the Naoro-Brown catchment area in the West Koiari district (S 9° 12.46' E 147° 34.45' and S 9° 10.35' E 147° 27.93'), on the south-eastern region of Papua New Guinea (Fig 1). This rapid assessment was conducted over six days as part of an Environmental Impact Assessment for a proposed mini-dam and hydro-power station [24]. The study area extends over highly forested riverine plains and foothills to lower montane forests. Rainfall is

seasonal, ranging between 1,550 – 2,000 mm yr<sup>-1</sup> and increases with elevation [20, 25]. Pristine vegetation dominates most of the study area, although it also includes patches of successional regrowth in old village and garden sites abandoned more than three decades ago.



**Fig. 1.** Orientation of the study sites showing the four forest types along a 13-km transect. The study area is dominated by small-crown hill forest with tracts of riverine mixed forests and lower montane forests associated with waterways and low mountain peaks, respectively.

### Study design

We identified four forest types along the transect, using forest classifications for Papua New Guinea [20]. These were riverine mixed forest (~173 m above sea level [a.s.l]), hill forest (~665 m a.s.l), lower montane forest (~1,174 m a.s.l), and riverine succession forest (~874 m a.s.l). Riverine mixed forest generally extends from riverbanks, through ravines, and along the ascending ridges where it merges with hill forest. Hill forest covers most of the study area (Fig. 1), extending along the ascending ridge crest of low mountains where it meets patches of lower montane forest covering the highest crests within the area. Unlike these three forest types, which are currently intact, riverine succession forests are patches of post-disturbance regrowth in abandoned human settlements along the Naoro-Brown river.

The topographical aspects defining each forest type were fairly distinctive.

Four 50 x 20 m (0.1 ha) plots were randomly established >0.1 km apart in each forest type. Topography within each plot was measured by elevation, linear distance between plots, and slope, as these have shown to be ecologically meaningful in complex landscapes [26-28]. Elevation above sea level and the

distance between each pair of plots were measured in the centre of each plot using a Garmin GPSmap 76Cx. Slope of each plot was estimated using a clinometer by averaging five slope measurements at randomly selected points along the direction of the greatest slope [29].

#### *Forest structure survey*

Forest structure was measured by tree height, stand density, and biomass. For each plot tree height was measured using a Haglöf ECII Electronic Clino / Height Meter. We measured and recorded all living trees  $\geq 10$  cm DBH, according to Pearson et al. [30], and enumerated all measured stems to determine the tree-stand density. Tree biomass was estimated using a generic allometric equation for tropical forests adapted from Chave et al. [31], and plot-level biomass was generated by summing values for all trees in each plot. Forest height was the average maximum tree height recorded at five random points within each plot.

#### *Plant survey*

Plant diversity was estimated via plant species richness and the Shannon-Wiener diversity index [32]. Compositional similarity among forest types was used as a proxy for *beta* diversity [14]. We collected voucher specimens of all tree morphospecies and tagged each tree for identification purposes. Voucher specimens were also collected for non-tree species (herbs, shrubs, climbers, creepers, and ferns) and treelets in each plot. All non-tree plants were sampled using twenty 1 x 1 m quadrats randomly placed within each plot (after Katovai et al. [33]). Flowers and fruiting bodies were collected where possible to assist with identification. Vouchers were taken to Pacific Adventist University, Port Moresby, for further taxonomical sorting and then to the National Herbarium at the Forest Research Institute in Lae for expert verification. All voucher specimens were keyed to genus and to species level where possible. A species list for each plot was then generated (Appendix A) and used to compare species compositional similarity among forest types. Saplings were excluded from the survey due to challenges in taxonomical sorting.

#### *Statistical Analysis*

A one-way analysis of variance (ANOVA) was used to test whether forest structure and species diversity variables differed among forest types, followed by Tukey's HSD tests to assess pair-wise differences. All analyses were run in SPSS [34].

We ran an analysis of similarity (ANOSIM) based on Bray–Curtis similarity matrices of species occurrence to determine how plant community composition varied among forest types [35-36]. We then used non-metric multi-dimensional scaling (NMDS) to identify major gradients in species composition. These analyses were carried out using PRIMER V6 [36].

To examine the effect of topography on plant endemism in the forest types, we categorised all species found in each plot into tree and non-tree categories. Using these categories, we estimated local endemism, the proportions of trees and non-trees occurring uniquely in a single forest type. Pearson correlations were used to test for associations among the arcsine-transformed endemism levels and log-transformed values of slope and elevation. Based on the correlation outputs, we selected highly associated predictor-response combinations ( $r > 0.70$ ), and used linear regressions to examine how topography influenced variation in local plant endemism within the Naoro-Brown landscape.

## Results

In total, we sampled 1.6 ha in the Naoro-Brown catchment area and identified 163 species (87 non-tree and 76 tree species) from 60 families, of which 93 were identified to species level (Appendix A). We also counted 754 trees with DBH  $\geq 10$  cm across the forest types. The estimated mean ( $\pm$ SD) of tree biomass for the entire area was  $537 \pm 356$  tonnes/ha.

### Forest structure and diversity

Forest structure differed among forest types, although results varied among response variables (Table 1). For example, while there were overall significant differences in mean tree height ( $F_{3, 12} = 68.8$ ,  $p < 0.0001$ ), tree stand density ( $F_{3, 12} = 43$ ,  $p < 0.0001$ ), and tree biomass ( $F_{3, 12} = 110$ ,  $p < 0.0001$ ), Tukey's tests showed different groupings of forest types associated with each measure (Table 1). Tree height, for instance, showed two homogenous groups. One group consisted of riverine mixed forest ( $31.6 \pm 1.4$  m) and hill forest ( $25.9 \pm 0.7$  m), and the other consisted of riverine succession ( $22.8 \pm 0.6$  m) and lower montane forest ( $21.2 \pm 1.4$  m). Mean tree density in riverine succession forest was significantly higher than in the three primary forests (Table 1). Riverine mixed forest had the highest mean biomass ( $1,113 \pm 141$  tonnes), followed by homogenous groups hill forest ( $442 \pm 32$  tonnes) and lower montane forest ( $315 \pm 24$  tonnes). Mean biomass of riverine succession forests was lowest ( $277 \pm 27$  tonnes), and differed significantly from all others (Table 1).

Table 1. Details of landscape, floristics and forest structure variables across forest types in the Naoro-Brown catchment. Mean values  $\pm$ SD of four 0.1ha plots per forest type are given for each variable. Superscript letters beside mean numbers of variables indicate significant pair-wise differences across forest types and elevation bands using Tukey's HSD tests. Means with different superscript letters are significantly different. Forest type acronyms explained: RSF = Riverine succession forest, LMF = Lower montane forest, HF = Hill forest and RMF = Riverine mixed forest.

Forest-type	Mean Species richness	Shannon Index	Est. Forest height (m)	Tree stand density	Est. Mean biomass (t)
RSF	$31 \pm 2.2^D$	$2.60 \pm 0.09^B$	$22.8 \pm 0.6^C$	$62.3 \pm 4.6^A$	$277.4 \pm 26.8^C$
LMF	$44.8 \pm 1.0^C$	$2.73 \pm 0.15^B$	$21.2 \pm 1.4^C$	$41.3 \pm 1.5^B$	$314.9 \pm 24.3^{BC}$
HF	$50.3 \pm 2.6^B$	$3.07 \pm 0.04^A$	$25.9 \pm 0.7^B$	$47 \pm 1.8^B$	$441.5 \pm 31.9^B$
RMF	$55.3 \pm 1.9^A$	$3.24 \pm 0.09^A$	$31.6 \pm 1.4^A$	$41.5 \pm 3.1^B$	$1113.2 \pm 141^A$

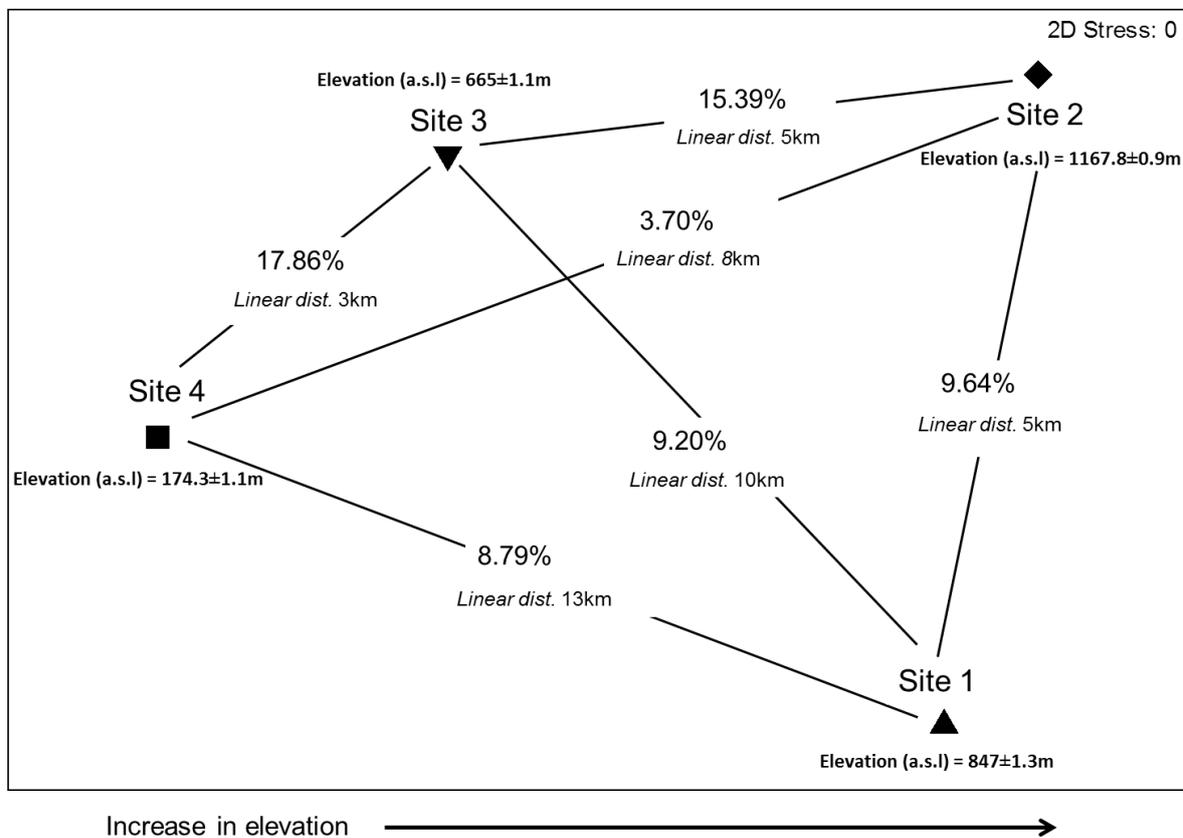
Plant diversity also differed among forest types (Table 1). Mean species richness differed significantly among forest types ( $F_{3, 12} = 69.3$ ,  $p < 0.0001$ ), with all pairwise comparisons being considerably different (Table 1). Riverine mixed forest had the highest mean richness ( $55.3 \pm 1.9$  species), followed by hill ( $50.3 \pm 2.6$  species), lower montane ( $44 \pm 1.0$  species), and riverine succession forests ( $31 \pm 2.1$  species). Shannon diversity indices also differed significantly among the forest types ( $F_{3, 12} = 38.1$ ,  $p < 0.000$ ), with Tukey's tests revealing two homogeneous subsets: riverine mixed forests ( $3.24 \pm 0.09$ ) and hill forests ( $3.07 \pm 0.04$ ); and lower montane forests ( $2.73 \pm 0.15$ ) and riverine succession forests ( $2.60 \pm 0.09$ ).

*Beta diversity*

ANOSIM and pairwise comparisons revealed that species composition differed significantly among forest types  $P < 0.001$ ; Fig 2). As expected, species compositional similarity was highest between hill forest and riverine mixed forest, albeit still with a relatively low similarity of 17.86%. Compositional similarity was lowest between riverine mixed forest and lower montane forest, with 3.70% similarity (Fig 2).

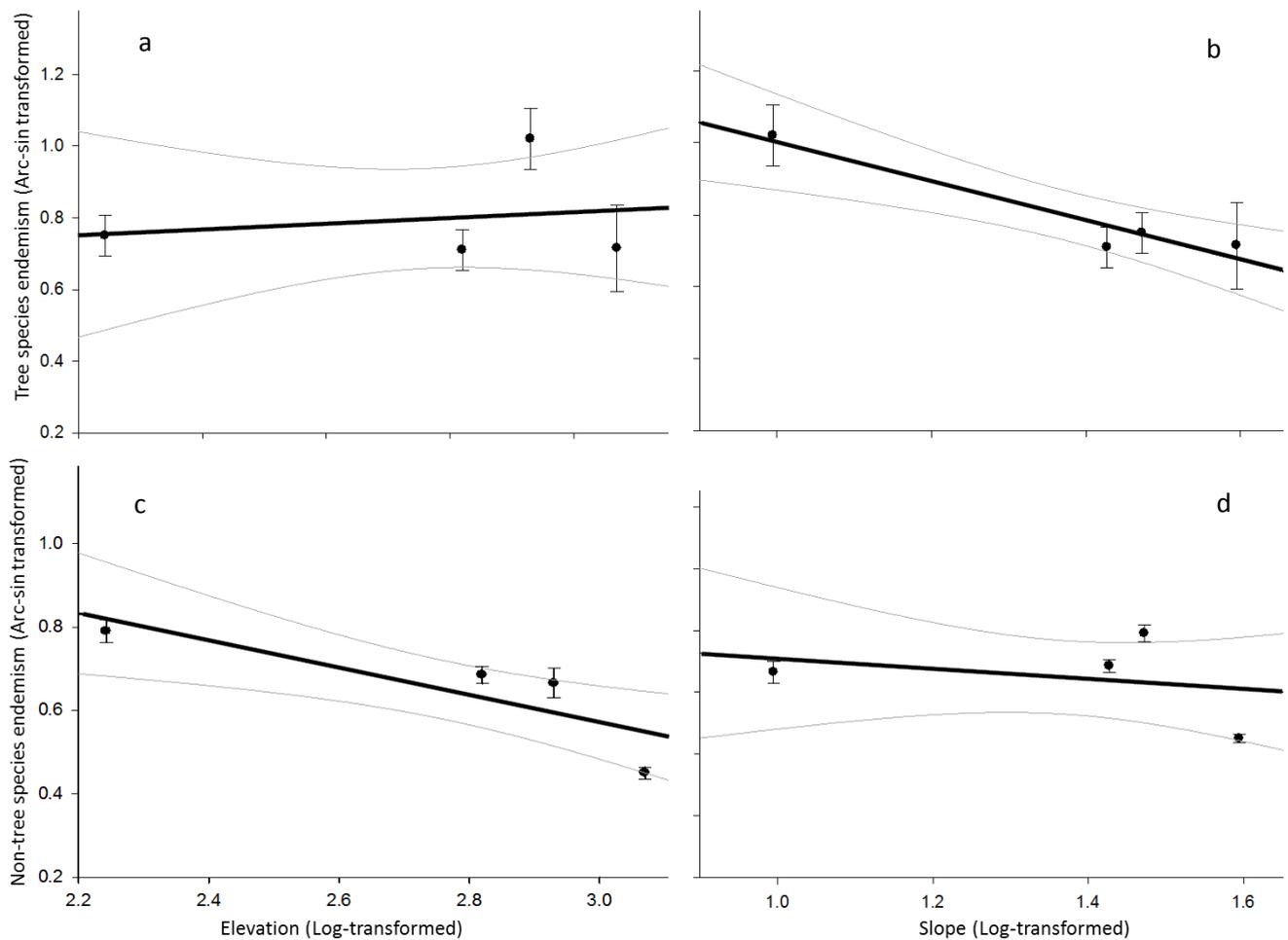
*Topography and local endemism*

Tree species endemism was strongly negatively associated with slope ( $r = -0.82, p < 0.001$ ), but its association with elevation was non-significant ( $r = 0.20, p > 0.05$ ). In contrast, non-tree endemism was highly negatively associated with elevation ( $r = -0.87, p < 0.001$ ) but not with slope ( $r = -0.15, p > 0.05$ ; all Pearson correlations).



**Fig. 2. Multidimensional Scaling (MDS) for similarity in species composition between Riverine successional forest (▲), Lower montane forest (◆), Hill forest (▼) and Riverine mixed forest (■). MDS is based on Bray–Curtis similarity indices. Also displayed are the species compositional similarity percentage and linear geographic distance (in km) between each forest type. The elevation gradient along the horizontal axis shows how forest types are positioned with respect to topographical elevation within the landscape.**

Linear regressions showed that elevation was a good predictor of local endemism for non-tree species ( $F_{1,14} = 102.7, p < 0.001$ ), explaining 87% of the variability in non-tree endemism among forest types (Fig 3c). Local endemism in trees was predicted by slope ( $F_{1,14} = 28.92, p < 0.001$ ), explaining 65% of the total variation among forest types (Fig 3b).



**Fig. 3. The regression plots (with 95% Confidence Intervals – in grey) display relationships between tree and non-tree local endemism across elevation and slope in the Naoro-Brown catchment area. Solid lines in b and c indicate the strong effects of elevation and slope on non-tree species and tree species endemism respectively. In contrast, solid lines in a and d indicate insignificant relation between the compared variables.**

## Discussion

### *Forest structure and diversity across forest types*

Forest structure and plant diversity were highly variable in our study transect (Table 1, Fig. 2). Such high spatial variation could result from both local environmental factors, such as varying precipitation, temperature, and topographical features [29, 37], as well as from different dynamics and disturbance histories throughout the study area [38]. Below we consider key attributes of each of these four major forest types.

### *Riverine mixed forest*

In riverine mixed forest, canopy trees are relatively uniform in height, averaging 31 m. This forest has large tree crowns that significantly reduce the amount of light penetrating into the understory and forest floor. Common trees are mainly from the genera *Syzygium*, *Litsea*, *Aglaia*, *Harpullia* (Tulipwood), and *Acalypha* (Copperleaf), with no evidence of single-species dominance. The dense canopy cover and leaf litter on the forest floor help to maintain surface moisture [39], which supports moss growth covering the base of trees and a high abundance of herbaceous forms. Large woody vines throughout the forest column are also apparent, which may indicate a mature forest system [40-42].

We observed a low density of treefall gaps in this forest type, which suggests only sporadic disturbance from wind or tree death. Treefall gaps displayed a range of seral stages, augmenting plant species diversity [43-44]. Perhaps a more substantial form of disturbance is triggered by huge volumes of runoff channelled through ravines that flood the forest floor during monsoonal rains between October and January. These ravines develop micro-topographical formations on the forest floor that could help diversify microhabitats within the forest [15, 45].

### *Hill forest*

Hill forests mainly contain small-crowned deciduous trees, thus having a relatively open canopy with tree heights rarely exceeding 28 m. Understory trees are abundant because understory light levels are relatively high [44]. Common deciduous trees include *Bombax ceiba* (Bombax), *Gordonia papuana* (Gordiana), *Pterocarpus spp.* (Makua or Nara) and *Terminalia spp* (Terminalia). The shrub layer is dominated by scrambled bamboo, *Maniltoa psilogyne*, and a variety of lianas and palm species that may be maintained by relatively high light and semi-dry conditions of the understory [46-47]. The rarity of herbaceous forms may also be related to such dry environmental conditions.

### *Lower montane forest*

In lower montane forests the trees exhibit smaller crowns than those at lower elevations. Mean canopy tree height was ~21 m with a few scattered *Syzygium trees* over 25 m high. Due to the small crowns and high variance in canopy height, light penetration into the understory and forest floor is irregular, creating large variability in the structure of the undergrowth. Trees dominating the canopy and sub-canopy mostly belong to the genera *Garcinia*, *Harpullia* (Tulipwood), *Cryptocarya*, *Macaranga* (Euphorbs), and *Syzygium*. The understory mainly includes a few genera of palms (*Calamus*, *Caryota*, *Hydriastile*), pandanas (*Freycinetia*) and a number of ground orchids in the genera *Tropidia* and *Bulbophyllum*.

### *Riverine successional forest*

After fallow decades, riverine successional forest mainly exhibited a high abundance of thin trees dominated by *Terminalia*, *Glochidion*, *Cryptocarya*, and a few *Ficus* species. Also present were multi-phase successional trees (*Litsea timoriana*, *Annesijoa novoguineensis*, *Dysoxylum* [Rose Mahogany],

*Xylopia papuana*), ferns, herbaceous creepers and shade-tolerant understory species, such as epiphytes and non-woody climbers. These varied groups indicate a mixing of plant life forms and successional stages in this forest.

### *Beta diversity and endemism*

The low species compositional similarity among these forests suggests high *beta* diversity in the Naoro-Brown catchment area (Fig 2). However, other tropical studies at comparable geographical distance (0-13km) reported lower species turnover of ~50% [e.g. 27-28, 48-50]. The high *beta* diversity in our study area may have been overestimated due to limited sampling, restricted to trees  $\geq 10$  cm DBH only. The large gradient in elevation along our transect (~1,000 m) would likely have enhanced *beta* diversity relative to the aforementioned studies, which were conducted over topographically less variable areas.

Our results also suggest that topography strongly influences local endemism of plant species. Such responses are generally regulated by microclimate and soil attributes along topographical gradients [e.g. 51-53]. However, consistent trends of plant endemism have been reported on larger spatial scales. For example, studies on oceanic islands have revealed a unimodal response to elevation whereby endemism peaks at mid-elevation and then gradually decreases at high elevations [58-59]. Relatively low diversification and speciation at high elevations on recently uplifted mountains may have caused in these patterns [59]. Our results cannot account for this because of the relatively small spatial extent of our study and its location. We suggest that the ecological mechanisms driving shifts in plant endemism vary at any given time and space due to complex interactions among environmental variables throughout the studied landscape [54-55].

### **Implications for conservation**

Our findings suggest that to conserve biological and functional diversity in New Guinea, protected areas must at least include landscapes that best represent the topographical variability throughout the island [2, 21, 33]. Immediate efforts should focus on forests that are most vulnerable to deforestation and degradation (see [2, 22]). Rapid plant surveys can be used opportunistically to document vital information on spatial vegetation patterns of uncharted landscapes in New Guinea. In the absence of such information, a focus on maximizing the conservation of gradients spanning topographic, geological, and climatic gradients should be a priority. For an island rich in locally endemic species that is being rapidly altered by a range of human land uses, such simple surrogate variables can help to guide near-term conservation efforts.

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### **References**

- [1] Haberle, S. G. 2007. Prehistoric human impact on rainforest biodiversity in highland New Guinea. *Philosophical transactions. Biological Sciences* 362: 219–228.
- [2] Shearman, P. and Bryan, J. 2011. A bioregional analysis of the distribution of rainforest cover, deforestation and degradation in Papua New Guinea. *Austral Ecology* 36: 9–24.
- [3] Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology Evolution and Systematics* 5:161–182.

- [4] McKnight, M. W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S. and Stuart, S. N. 2007. Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biology* 5: e272.
- [5] McGavin, G. 2009. *Scientific expedition to mount Bosavi, southern highlands, Papua New Guinea (REPORT)*. Oxford University Museum of Natural History and the Department of Zoology, Oxford University, UK. [http://downloads.bbc.co.uk/springwatch/llotv\\_finalreport\\_20090907.pdf](http://downloads.bbc.co.uk/springwatch/llotv_finalreport_20090907.pdf) (accessed 12 June 2014).
- [6] Mack, A. L. Editor. 1998. *A biological assessment of the Lakekamu basin, Papua New Guinea*. 9 RAP Working Papers, Conservation International.
- [7] Richards, S. J. Editor. 2007. *A rapid biodiversity assessment of the Kaijende highlands, Enga province, Papua New Guinea*. RAP Bulletin of Biological Assessment 45. Conservation International, Arlington, VA, USA.
- [8] Richards, S. J. and Gamui, B. G. Editors. 2011. *Rapid biological assessments of the Nakanai Mountains and the upper Strickland basin: surveying the biodiversity of Papua New Guinea's sublime karst environments*. RAP Bulletin Biological Assessment 60.
- [9] Frodin, D. G. 1990. Botanical progress in Papuasia. In: Baas, P., Kalkman, K., and Geesink, R. Editors. *The plant diversity of Malesia, Proceedings of the Flora Malesiana Symposium Commemorating Prof. Dr. C.G.G.J. van Steenis*. Kluwer Academic Publishers. Dordrecht, Netherlands. Pp 235–247.
- [10] Novotny, V et al. 2010. Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. *Journal of Animal Ecology* 79: 1193–1203.
- [11] Novotny, V. 2009. Beta diversity of plant–insect food webs in tropical forests: a conceptual framework. *Insect Conservation and Diversity* 2: 5–9.
- [12] Novotny, V. et al. 2007. Low beta diversity of herbivorous insects in tropical forests. *Nature* 448: 692–695.
- [13] Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338.
- [14] Legendre, P. and De Caceres, M. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters* 16: 951–963.
- [15] Wright, D. D. Jessen, J. H., Burke, P., and Garza, H. G. 1997. Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica* 29: 250–260.
- [16] Weiblen, G. D. 1998. Composition and structure of a one hectare forest plot in the Crater Mountain Wildlife Management Area, Papua New Guinea. *Science in New Guinea* 24, 23–32.
- [17] Harrison, R. D. 2005. Figs and the diversity of tropical rainforests. *BioScience* 55:1053–1064.
- [18] Takeuchi, W. 2007. Vascular plants of the Kaijende Highlands, Papua New Guinea: Taxonomic and vegetation survey. A Rapid Biodiversity Assessment of the Kaijende Highlands, Enga Province, Papua New Guinea 25–39.
- [19] Keppel, G., Buckley, Y. M. and Possingham, H. P. 2010. Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *Journal of Ecology* 98: 87–95.
- [20] Paijmans, K. 1975. *Vegetation of Papua New Guinea*.
- [21] Faith, D. P., Margules, C. R., Walker, P. A., Stein, J. and Natera, G. 2001. Practical application of biodiversity surrogates and percentage targets for conservation in Papua New Guinea. *Pacific Conservation Biology* 6: 289–303.
- [22] Nicholls, S. 2004. *The priority environmental concerns of Papua New Guinea*. Marfleet Printing. Apia, Samoa.
- [23] Baraloto, C., Molto, Q., Rabaud, S., Héroult, B., Valencia, R., Blanc. L., Fine. P. V. A. and Thompson, J. 2013. Rapid simultaneous estimation of aboveground biomass and tree diversity across neotropical forests: A comparison of field inventory methods. *Biotropica* 45: 288–298.

- [24] Katovai, E. and Saguba, P. 2010. *Baseline Environmental study for the Naoro-Brown river hydro project (REPORT)*. Pacific Adventist University Science and Technology Consultancy Team. Port Moresby, Papua New Guinea.
- [25] World weather and climate 2010-2013. <http://www.weather-and-climate.com/>(accessed 23 September 2014).
- [26] Yasuhiro, K., Hirofumi, M. and Kihachiro, K. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *Journal of Ecology* 92: 230–240.
- [27] Apgaua, D. M. G., Coelho, P.A., dos Santos, R. M., Santos, P. F. and de Oliveira-Filho, A. T. 2014. Tree community structure in a seasonally dry tropical forest remnant, Brazil. *Cernea* 20: 173–182.
- [28] Arellano, G. and Macía, M. 2014. Local and regional dominance of woody plants along an elevational gradient in a tropical montane forest of northwestern Bolivia. *Plant Ecology* 215: 39–54.
- [29] Clark, D. B. and Clark, D. A. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* 137: 185–198.
- [30] Pearson, T., Walker, S. and Brown, S. 2013. *Sourcebook for land use, land-use change and forestry projects*. Washington DC; World Bank. <http://documents.worldbank.org/curated/en/2013/01/18009480/sourcebook-land-use-land-use-change-forestry-projects> (accessed 12 January 2014).
- [31] Chave, J., Riéra, B., Dubois, M. 2001. Estimation of biomass in a Neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology* 17, 79–96.
- [32] Asase, A., Asiatokor, B. and Ofori-Frimpong, K. 2014. Effects of selective logging on tree diversity and some soil characteristics in a tropical forest in southwest Ghana. *Journal of Forestry Research* 25: 171–176.
- [33] Katovai, E., Burley, A. and Mayfield, M. M. 2012. Understory plant species and functional diversity in the fragmented wet tropical forests of Kolombangara, Solomon Islands. *Biological Conservation* 145: 214–224.
- [34] IBM Corp. Released. 2013. *IBM SPSS Statistics for Windows, Version 22.0*. Armonk, NY: IBM Corp.
- [35] Bray, J. R. and Curtis, J. T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27, 326–349.
- [36] Clarke, K. R. and Gorley, R. N. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- [37] Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances, perspectives in plant ecology. *Evolution and Systematics* 6: 51–71.
- [38] Pukkala, T. and Gadaw, K. 2012. *Continuous Cover Forestry (2nd eds)*. *Managing Forest Ecosystems* 23.
- [39] Xiong, S. J., Johansson, M. E., Hughes, F. M. R., Hayes, A., Richards K. S. and Nilsson C. 2003. Interactive effects of soil moisture, vegetation canopy, plant litter and seed addition on plant diversity in a wetland community. *Journal of Ecology* 91: 976–986.
- [40] Putz, F. E. 1983. Liana biomass and leaf area of a “tierra firme” forest in the Rio Negro basin, Venezuela. *Biotropica* 15:185–189.
- [41] Allen, B. P., Sharitz, R. R. and Goebel, P. C. 2005. Twelve years post-hurricane liana dynamics in an old-growth southeastern floodplain forest. *Forest Ecology and Management* 218: 259–269.
- [42] DeWalt, S., Ickes, K., Nilus, R., Harms, K. and Burslem, D. R. P. 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecology* 186: 203–216.
- [43] Denslow, J. S. 1995. Disturbance and diversity in tropical rain forests: The density effect. *Ecological Applications* 5: 962–968.
- [44] Letcher, S.G. and Chazdon, R. L. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41: 608–617.

- [45] Wright, J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.
- [46] Schnitzer, S. A. and Bongers, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17: 223–230.
- [47] Cintra, R., Ximenes, A. D. C., Gondim, F.R. and Kropf, M. S. 2005. Forest spatial heterogeneity and palm richness, abundance and community composition in terra firme forest, central Amazon. *Brazilian Journal of Botany* 28: 75–84.
- [48] Condit, R, et al. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666-669.
- [49] Pennington, R. T., Lavin, M., Oliveira, A. 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology Evolution and Systematics* 40: 437–457.
- [50] Toledo, M., Poorter, L., Pena-Claros, M., Alarcon, A., Balcazar, J., Leano, C., Licona J. C., Bongers, F. 2011. Climate and soil drive forest structure in Bolivian lowland forests. *Journal of Tropical Ecology* 27: 333–345.
- [51] Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B. and Thomas, C. D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.
- [52] Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L. and Mayaux, P. 2013. African rainforests: past, present and future. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368.
- [53] Lippok, D., Beck, S. G., Renison, D., Hensen, I., Apaza, A. E. and Schleuning, M. 2014. Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. *Journal of Vegetation Science* 25: 724–733.
- [54] Warren, R. J. 2008. Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. *Plant Ecology* 198: 297-308.
- [55] Bonetti, M. F and Wiens, J. J. 2014. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proc. R. Soc.* 281.
- [56] Whitfeld, T. J. S., Kress, W. J., Erickson, D. L., Weiblen, G. D. 2012. Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography* 35: 821-830.
- [57] Whitfeld, T. J. S., Lasky, J. R., Damas, K., Sosanika, G., Molem, K., Montgomery, R. A. 2014. Species richness, forest structure, and functional diversity during succession in the New Guinea lowlands. *Biotropica* 46: 538-548.
- [58] Trigas, P., Panitsa, M., Tsiftsis, S. 2013. Elevational gradient of vascular plant species richness and endemism in Crete – The effect of post-isolation mountain uplift on a continental Island system. *PLoS ONE* 8(3): e59425.
- [59] Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. *Journal of Biogeography* 29: 1159–1165.

**Appendix A. Identified plant taxa collected in the study area.**

Sp. NO.	Family	Genera	Species
1	<i>Actinidiaceae</i>	<i>Saurauia</i>	<i>conferta</i>
2	<i>Actinidiaceae</i>	<i>Saurauia</i>	<i>sp.</i>
3	<i>Amaryllidaceae</i>	<i>Crimun</i>	<i>asiatica</i>
4	<i>Anacardiaceae</i>	<i>Semecarpus</i>	<i>sp.</i>
5	<i>Annonaceae</i>	<i>Cyathocalyx</i>	<i>petiolatus</i>
6	<i>Annonaceae</i>	<i>Cyathocalyx</i>	<i>sp.</i>
7	<i>Annonaceae</i>	<i>Polyalthia</i>	<i>glanca</i>
8	<i>Annonaceae</i>	<i>Xylopia</i>	<i>papuana</i>
9	<i>Apocynaceae</i>	<i>Allamanda</i>	<i>sp.</i>
10	<i>Apocynaceae</i>	<i>Papuechites</i>	<i>sp.</i>
11	<i>Araceae</i>	<i>Homalomena</i>	<i>cordata</i>
12	<i>Araceae</i>	<i>Pothos</i>	<i>hellwigii</i>
13	<i>Araceae</i>	<i>Rhaphidophora</i>	<i>peekelii</i>
14	<i>Araceae</i>	<i>Rhaphidophora</i>	<i>sp.</i>
15	<i>Araliaceae</i>	<i>Polyscias</i>	<i>sp.</i>
16	<i>Araliaceae</i>	<i>Schefflera</i>	<i>sp.</i>
17	<i>Arecaceae</i>	<i>Calamus</i>	<i>hollrungii</i>
18	<i>Arecaceae</i>	<i>Caryota</i>	<i>rumphiana</i>
19	<i>Arecaceae</i>	<i>Heterospath</i>	<i>sp.</i>
20	<i>Arecaceae</i>	<i>Hydriastele</i>	<i>costata</i>
21	<i>Arecaceae</i>	<i>Hydriastele</i>	<i>sp.1</i>
22	<i>Arecaceae</i>	<i>Hydriastele</i>	<i>sp.2</i>
23	<i>Asclepiadaceae</i>	<i>Hoya</i>	<i>sp.1</i>
24	<i>Asclepiadaceae</i>	<i>Hoya</i>	<i>sp.2</i>
25	<i>Aspleniaceae</i>	<i>Asplenium</i>	<i>nidus</i>
26	<i>Aspleniaceae</i>	<i>Vittaria</i>	<i>sp.</i>
27	<i>Asteraceae</i>	<i>Elaphantopus</i>	<i>scaber</i>
28	<i>Bombacaceae</i>	<i>Bombax</i>	<i>ceiba</i>
29	<i>Burseraceae</i>	<i>Canarium</i>	<i>acutifolium</i>
30	<i>Clusiaceae</i>	<i>Garcinia</i>	<i>sp.1</i>
31	<i>Clusiaceae</i>	<i>Garcinia</i>	<i>sp.2</i>
32	<i>Combretaceae</i>	<i>Terminalia</i>	<i>sp.</i>
33	<i>Cyperaceae</i>	<i>Cyperus</i>	<i>rotundus</i>
34	<i>Cyperaceae</i>	<i>Fimbristylis</i>	<i>dichotoma</i>
35	<i>Davalliaceae</i>	<i>Drynaria</i>	<i>sp.</i>

36	<i>Davalliaceae</i>	<i>Lindsaea</i>	<i>sp.</i>
37	<i>Davalliaceae</i>	<i>Nephrolepis</i>	<i>hirsutula</i>
38	<i>Dioscoreaceae</i>	<i>Dioscorea</i>	<i>alata</i>
39	<i>Dracaenaceae</i>	<i>Dracaena</i>	<i>angustifolia</i>
40	<i>Ebenaceae</i>	<i>Diospyros</i>	<i>sp.</i>
41	<i>Ebenaceae</i>	<i>Diospyros</i>	<i>sogerensis</i>
42	<i>Ericaceae</i>	<i>Dimorphanthera</i>	<i>dekokii</i>
43	<i>Euphorbiaceae</i>	<i>Acalypha</i>	<i>sogerensis</i>
44	<i>Euphorbiaceae</i>	<i>Antidesma</i>	<i>sp.</i>
45	<i>Euphorbiaceae</i>	<i>Codiaeum</i>	<i>variegatum</i>
46	<i>Euphorbiaceae</i>	<i>Drapetes</i>	<i>bordenii</i>
47	<i>Euphorbiaceae</i>	<i>Glochidion</i>	<i>cf. ferdinandi</i>
48	<i>Euphorbiaceae</i>	<i>Glochidion</i>	<i>phillipicum</i>
49	<i>Euphorbiaceae</i>	<i>Macaranga</i>	<i>punchata</i>
50	<i>Euphorbiaceae</i>	<i>Phyllanthus</i>	<i>sp.</i>
51	<i>Euphorbiaceae</i>	<i>Pimelodendron</i>	<i>amboinicum</i>
52	<i>Fabaceae</i>	<i>Archidendron</i>	<i>glabrum</i>
53	<i>Fabaceae</i>	<i>Desmodium</i>	<i>sp.</i>
54	<i>Fabaceae</i>	<i>Gigasiphon</i>	<i>schlechterii</i>
55	<i>Fabaceae</i>	<i>Maniltoa</i>	<i>psylogyne</i>
56	<i>Fabaceae</i>	<i>Maniltoa</i>	<i>sp.</i>
57	<i>Fabaceae</i>	<i>Milletia</i>	<i>pinnata</i>
58	<i>Fagaceae</i>	<i>Lithocarpus</i>	<i>celebicus</i>
59	<i>Flacourtiaceae</i>	<i>Casearia</i>	<i>sp.</i>
60	<i>Flagellariaceae</i>	<i>Flagellaria</i>	<i>indica</i>
61	<i>Gesneriaceae</i>	<i>Cyrtandra</i>	<i>erectiloba</i>
62	<i>Gleicheniaceae</i>	<i>Dicranopteris</i>	<i>linearis</i>
63	<i>Hypoxidaceae</i>	<i>Curculigo</i>	<i>recurvata</i>
64	<i>Lauraceae</i>	<i>Cryptocarya</i>	<i>sp.</i>
65	<i>Lauraceae</i>	<i>Endiandra</i>	<i>sp.1</i>
66	<i>Lauraceae</i>	<i>Endiandra</i>	<i>sp.2</i>
67	<i>Lauraceae</i>	<i>Litsea</i>	<i>timoriana</i>
68	<i>Lauraceae</i>	<i>Litsea</i>	<i>sp.1</i>
69	<i>Lauraceae</i>	<i>Litsea</i>	<i>sp.2</i>
70	<i>Liliaceae</i>	<i>Dianella</i>	<i>sp.</i>
71	<i>Liliaceae</i>	<i>Dianella</i>	<i>ensifolia</i>
72	<i>Loganiaceae</i>	<i>Strychnos</i>	<i>minor</i>
73	<i>Lycopodiaceae</i>	<i>Lycopodium</i>	<i>cernuum</i>

74	<i>Melastomataceae</i>	<i>Medinilla</i>	<i>crassinervia</i>
75	<i>Meliaceae</i>	<i>Aglaia</i>	<i>sp.</i>
76	<i>Meliaceae</i>	<i>Chisocheton</i>	<i>sp.</i>
77	<i>Meliaceae</i>	<i>Dysoxylum</i>	<i>sp.1</i>
78	<i>Meliaceae</i>	<i>Dysoxylum</i>	<i>sp.2</i>
79	<i>Menispermaceae</i>	<i>Tinospora</i>	<i>sp.</i>
80	<i>Monimiaceae</i>	<i>Kibara</i>	<i>fugax</i>
81	<i>Monimiaceae</i>	<i>Palmeria</i>	<i>sp.</i>
82	<i>Monimiaceae</i>	<i>Palmeria</i>	<i>brassii</i>
83	<i>Moraceae</i>	<i>Artocarpus</i>	<i>communis</i>
84	<i>Moraceae</i>	<i>Ficus</i>	<i>sp.1</i>
85	<i>Moraceae</i>	<i>Ficus</i>	<i>sp.2</i>
86	<i>Moraceae</i>	<i>Ficus</i>	<i>sp.3</i>
87	<i>Moraceae</i>	<i>Ficus</i>	<i>sp.4</i>
88	<i>Moraceae</i>	<i>Ficus</i>	<i>molior</i>
89	<i>Myristicaceae</i>	<i>Gymnacranthera</i>	<i>paniculata var. zippelliana</i>
90	<i>Myrsinaceae</i>	<i>Maesa</i>	<i>haplobotrys</i>
91	<i>Myrsinaceae</i>	<i>Rapanea</i>	<i>leucantha</i>
92	<i>Myrtaceae</i>	<i>Syzygium</i>	<i>plumeum</i>
93	<i>Myrtaceae</i>	<i>Syzygium</i>	<i>acuminatissima</i>
94	<i>Myrtaceae</i>	<i>Syzygium</i>	<i>malaccense</i>
95	<i>Myrtaceae</i>	<i>Syzygium</i>	<i>longipes</i>
96	<i>Myrtaceae</i>	<i>Syzygium</i>	<i>claviflorum</i>
97	<i>Oleaceae</i>	<i>Chionanthus</i>	<i>brassii</i>
98	<i>Oleaceae</i>	<i>Chionanthus</i>	<i>sessiliflorum</i>
99	<i>Orchidaceae</i>	<i>Bulbophyllum</i>	<i>sp.</i>
100	<i>Orchidaceae</i>	<i>Dendrobium</i>	<i>sp.</i>
101	<i>Orchidaceae</i>	<i>Glossoryncha</i>	<i>sp.</i>
102	<i>Orchidaceae</i>	<i>Tropidia</i>	<i>disticha</i>
103	<i>Pandanaceae</i>	<i>Freycinetia</i>	<i>linearis</i>
104	<i>Pandanaceae</i>	<i>Freycinetia</i>	<i>sp.1</i>
105	<i>Pandanaceae</i>	<i>Freycinetia</i>	<i>sp.2</i>
106	<i>Piperaceae</i>	<i>Piper</i>	<i>macropiper</i>
107	<i>Piperaceae</i>	<i>Piper</i>	<i>sp.</i>
108	<i>Pittosporaceae</i>	<i>Pittosporum</i>	<i>sp.</i>
109	<i>Poaceae</i>	<i>Arundo</i>	<i>sp.</i>
110	<i>Poaceae</i>	<i>Bambusa</i>	<i>sp.</i>
111	<i>Poaceae</i>	<i>Coix</i>	<i>lachyma-jobi</i>

112	<i>Poaceae</i>	<i>Eriachne</i>	<i>sp.</i>
113	<i>Poaceae</i>	<i>Imperata</i>	<i>cylindrica</i>
114	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>
115	<i>Poaceae</i>	<i>Setaria</i>	<i>sp.</i>
116	<i>Polypodiaceae</i>	<i>Christella</i>	<i>arida (Don)</i>
117	<i>Polypodiaceae</i>	<i>Diplazium</i>	<i>sp.</i>
118	<i>Polypodiaceae</i>	<i>Drynaria</i>	<i>sp.</i>
119	<i>Polypodiaceae</i>	<i>Humata</i>	<i>pectinata (J.J.Sm)</i>
120	<i>Polypodiaceae</i>	<i>Lindsaea</i>	<i>repens (Bory)</i>
121	<i>Polypodiaceae</i>	<i>Microsorium</i>	<i>sp.3</i>
122	<i>Polypodiaceae</i>	<i>Microsorium</i>	<i>sp.1</i>
123	<i>Polypodiaceae</i>	<i>Microsorium</i>	<i>sp.2</i>
124	<i>Polypodiaceae</i>	<i>Nephrolepis</i>	<i>sp.</i>
125	<i>Polypodiaceae</i>	<i>Polypodium</i>	<i>sp.</i>
126	<i>Polypodiaceae</i>	<i>Pteris</i>	<i>cretica</i>
127	<i>Polypodiaceae</i>	<i>Pteris</i>	<i>sp.</i>
128	<i>Polypodiaceae</i>	<i>Sphaerostephanos</i>	<i>sp.1</i>
129	<i>Polypodiaceae</i>	<i>Sphaerostephanos</i>	<i>sp.2</i>
130	<i>Polypodiaceae</i>	<i>Sphaerostephanos</i>	<i>unitus</i>
131	<i>Polypodiaceae</i>	<i>Tectaria</i>	<i>siifolia (Wild)</i>
132	<i>Polypodiaceae</i>	<i>Tectaria</i>	<i>semibipinnata (Wall)</i>
133	<i>Polypodiaceae</i>	<i>Tectaria</i>	<i>sp.</i>
134	<i>Proteaceae</i>	<i>Helicia</i>	<i>sp.</i>
135	<i>Rhamnaceae</i>	<i>Ziziphus</i>	<i>angustifolius</i>
136	<i>Rhizophoraceae</i>	<i>Gynotroches</i>	<i>axillaris</i>
137	<i>Rosaceae</i>	<i>Prunus</i>	<i>gazel-peninsulae</i>
138	<i>Rubiaceae</i>	<i>Guettadella</i>	<i>sp.</i>
139	<i>Rubiaceae</i>	<i>Guettadella</i>	<i>sp.1</i>
140	<i>Rubiaceae</i>	<i>Lasianthus</i>	<i>sp.</i>
141	<i>Rubiaceae</i>	<i>Mussaenda</i>	<i>sp.</i>
142	<i>Rubiaceae</i>	<i>Psychotria</i>	<i>sp.1</i>
143	<i>Rubiaceae</i>	<i>Psychotria</i>	<i>sp.2</i>
144	<i>Sapindaceae</i>	<i>Cupaniopsis</i>	<i>sp.</i>
145	<i>Sapindaceae</i>	<i>Guioa</i>	<i>sp.</i>
146	<i>Sapindaceae</i>	<i>Guioa</i>	<i>crassinervia</i>
147	<i>Sapindaceae</i>	<i>Harpullia</i>	<i>sp.</i>
148	<i>Sapindaceae</i>	<i>Harpullia</i>	<i>longipetala</i>
149	<i>Sapotaceae</i>	<i>Palaquium</i>	<i>warburgianum</i>

<b>150</b>	<i>Sapotaceae</i>	<i>Manilkara</i>	<i>sp.</i>
<b>151</b>	<i>Schizaeaceae</i>	<i>Schizaea</i>	<i>dichotoma</i>
<b>152</b>	<i>Selaginellaceae</i>	<i>Selaginella</i>	<i>aspericaulis</i>
<b>153</b>	<i>Smilacaceae</i>	<i>Smilax</i>	<i>australis</i>
<b>154</b>	<i>Sterculiaceae</i>	<i>Sterculia</i>	<i>schumanniana</i>
<b>155</b>	<i>Sterculiaceae</i>	<i>Sterculia</i>	<i>papuana</i>
<b>156</b>	<i>Theaceae</i>	<i>Gordonia</i>	<i>papuana</i>
<b>157</b>	<i>Theaceae</i>	<i>Gordonia</i>	<i>sp.</i>
<b>158</b>	<i>Urticaceae</i>	<i>Elatostema</i>	<i>novoguiniense</i>
<b>159</b>	<i>Vitaceae</i>	<i>Leea</i>	<i>indica</i>
<b>160</b>	<i>Zingiberaceae</i>	<i>Alpinia</i>	<i>sp.</i>
<b>161</b>	<i>Zingiberaceae</i>	<i>Amomum</i>	<i>aculeatum</i>
<b>162</b>	<i>Zingiberaceae</i>	<i>Curcuma</i>	<i>longa</i>
<b>163</b>	<i>Zingiberaceae</i>	<i>Hornstedtia</i>	<i>scottiana</i>