Plant diversity and structure of the Caimpugan peat swamp forest on Mindanao Island, Philippines

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SUMMARY

This investigation examined the species diversity and vegetation structure of the peat swamp forest on Mindanao Island, Philippines in relation to peat thickness, hydrology and physicochemical properties of soil and water. Sampling plots were randomly established along a relatively straight transect from the eastern side of the fringing tall pole forest towards the inner zone of pygmy forest, as well as in forest on the Kasawangan lakeshore in the western part of the peatland. The results showed that additional previously unidentified vegetation zones could be distinguished between the tall pole forest and the pygmy forest; i.e. tall intermediate forest and low intermediate forest. Statistically, these additional zones were strongly supported by analysis of variance on stand structure and by non-metric multidimensional scaling on peat properties. Moreover, a *Lycopodium-Dicranopteris* dominated plant community, which occurs arbitrarily as patches, was also observed. The tall pole forest was the most diverse forest type. In total, 101 species belonging to 56 families and 81 genera of vascular plants (trees and understorey vegetation) were recorded, with *Tristaniopsis decorticata* (Myrtaceae) and *Thoracostachyum sumatranum* (Cyperaceae) being the most dominant. Changes in forest structure from the outer to the inner zone are related to the increase in peat thickness towards the centre of the dome. The changes in structure are influenced by the shallow superficial peat layer and the protective surface layer of the peatland, the acrotelm.

KEY WORDS: acrotelm, peatland, species composition

INTRODUCTION

In Southeast Asia, peatlands are found mostly at low altitudes, with extensive areas occurring in parts of Sumatra, the Malay Peninsula, Borneo (Kalimantan, Sarawak, and Brunei) and New Guinea (Page *et al.* 2006, 2012; Posa *et al.* 2011). In the Philippines, several estimates of peatland area have been completed (Andriesse 1988, Oravainen *et al.* 1992, Klemetti *et al.* 1996), but most of these peatlands have long been deforested and converted to agriculture or other uses (Davies 2006, Fernando *et al.* 2008). Only one site on Mindanao Island still contains a significant area of peat swamp forest; in the barangay (village) of Caimpugan, within the Agusan Marsh area in Agusan del Sur Province (Caraga Region). Until recently, the peat swamp forest here was very poorly known, having been only briefly described in the recent classification of Philippine forest formations by Fernando *et al.* (2008). In general, little or no work has been done on the flora, fauna, pedology and hydrology of peatlands in the Philippines, specifically in Mindanao, and no detailed account is available regarding the characteristics of the biophysical environment, its impact and dynamic role, and biodiversity in general (Davies 2006).

Many ecosystem functions and environmental services are provided by peat swamp forests. These include: supporting plants, animals, and microbial biodiversity; as hydrological catchments; and their critical role in terrestrial carbon storage (Page & Rieley 1998, Page *et al.* 2006, 2011, 2012; Posa *et al.* 2011). The very limited knowledge about peat swamp forest in the Philippines has impeded appreciation of this unique forest formation and, consequently, its effective conservation. The dearth of knowledge is reflected in the inadequate capacity of national and local government to manage peatlands wisely (Davies 2006), and there are no scientifically-based policies in place pertaining to peatlands and their appropriate management and conservation. In this article we help provide a foundation for developing such conservation policies by describing the plant species diversity, composition, structure, soil physicochemical and hydrological properties of the peat swamp forest in Caimpugan, along with the interdependence of these factors which define the physical appearance of the ecosystem.

METHODS

Study site

The study site is located in the peatland area of Barangay Caimpugan, Municipality of San Francisco, Agusan del Sur Province on Mindanao Island, Philippines (8° 21′ – 8° 27.5′ N, 125° 49.5′ – 125° 55′ E; Figure 1). The peatland is bounded by the Gibong River to the east and the Agusan River to the west, and lies approximately 30 km WSW from the nearest coastline in Barobo, Surigao del Sur Province. The peatland is part of the Agusan Marsh Wildlife Sanctuary (Mallari *et al.* 2001, CI-DENR-PAWB-Haribon 2006). It covers an area of 5,630 ha and spans two municipalities of Agusan del Sur Province, namely San Francisco and Talacogon. The Wildlife Gratuitous Permit No. R13-2010-002, issued on 02 July 2010 by the Philippine Department of Environment and Natural Resources (DENR) Regional Office in Butuan City, granted permission for field research and collection of vascular plant voucher specimens.

Sampling and data collection

Three vegetation zones consisting of tall pole, intermediate and pygmy forest have previously been recognised in the Caimpugan peatland by Davies (2006). However, the extent of the tall pole forest and its boundary with intermediate forest are poorly defined and often confusing. In contrast, the pygmy forest is clearly distinguished by a reduction in stem diameter and tree height (Davies 2006, Alibo & Lasco 2012). In this study, sampling plots were laid out starting near the edge and moving towards the centre of the peatland, choosing locations for the plots on the basis of apparent changes in stand structure. Twelve sampling plots were established within four perceived zones of tall pole, tall intermediate, low intermediate and pygmy forest. The additional zone of tall intermediate forest was situated between the tall pole and low intermediate forest zones, and consisted of trees with much smaller height and stem diameter than in tall pole forest. Three 10 × 20 m sampling plots were established in each of the first three zones at the

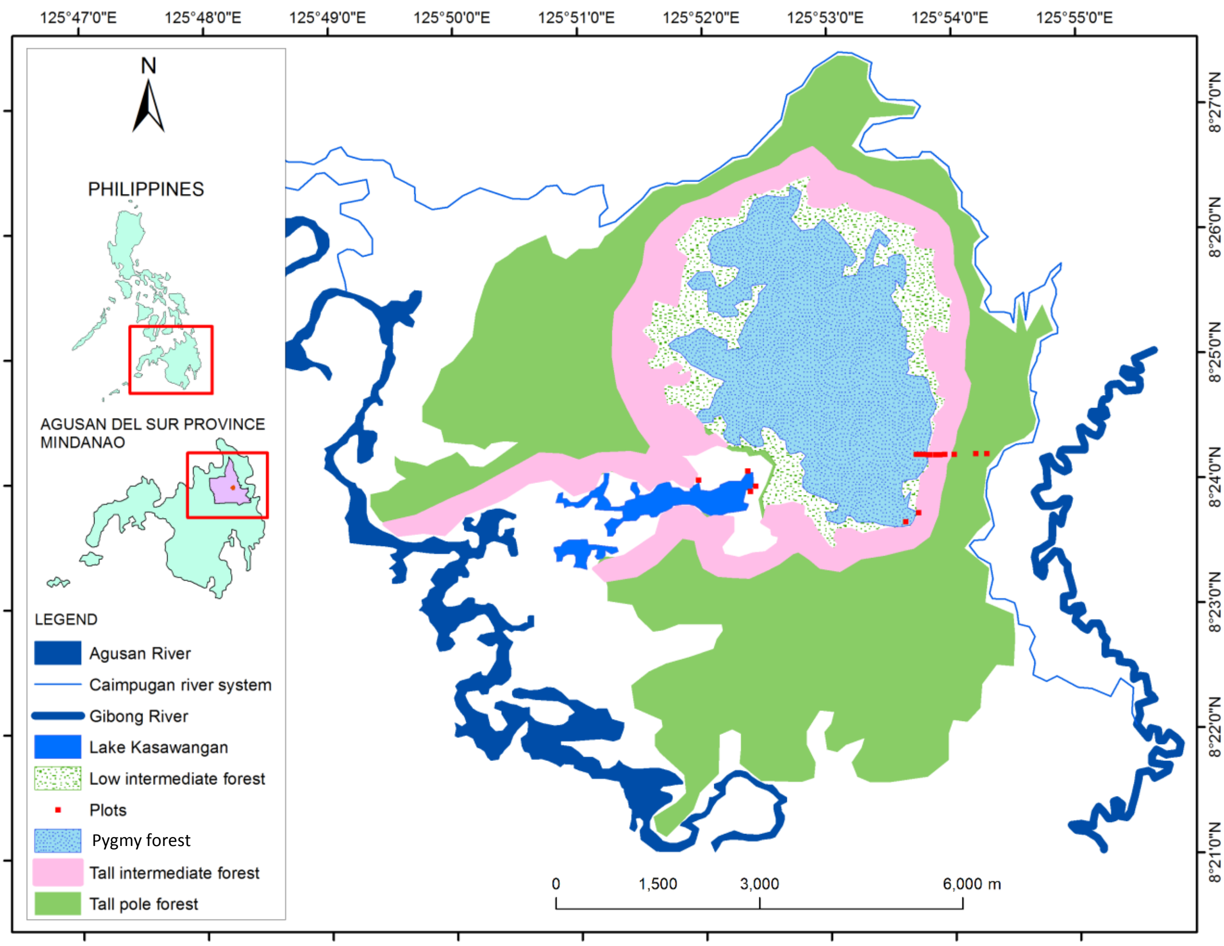

Figure 1. Map of the Caimpugan peat swamp forest, Agusan del Sur Province (lower inset) on Mindanao Island, Philippines (upper inset), showing the distribution of sampling plots.

eastern side of the peatland (Figure 1). In the pygmy forest towards the centre, sampling was conducted in three 10 × 10 m plots because of difficult access due to the presence of deep pools often exceeding knee depth. At the western side of the peat dome, four additional 10 × 10 m sampling plots were established in the forest on both sides of Lake Kasawangan. Two more sampling plots were established in a *Lycopodium-Dicranopteris* plant community found by the authors. This community was not mentioned by Davies (2006) and occurs in patches ranging in size from less than 10 m^2 to 2 ha. In summary, 18 sampling plots were set up in six different forest zones and vegetation communities, on both the eastern and western sides of the peatland area (Figure 1).

Measurement and identification of trees

Within each plot, all trees with stem diameter at least 2 cm at breast height (DBH) were measured and identified. The field measurements recorded were DBH, average crown diameter (calculated from two measurements from dripline to dripline per tree) and tree height (measured using a tree altimeter). The 2 cm DBH limit was chosen to allow incorporation of smaller trees into the dataset, particularly in the pygmy forest where DBH does not exceed 10 cm. The basal area (BA) of each tree was calculated using the formula $BA = 0.7854 \times (DBH)^2$ (Müller-Dombois & Ellenberg 1974). Trees were identified directly in the field but specimens were collected to confirm identification and for herbarium storage.

Measurements of understorey species

Three 1 × 1 m quadrats were randomly established within each sampling plot. All individual understorey plants found within each quadrat were measured and recorded with species name and percent ground cover.

Incidental species sampling

Species observed within 2–5 m of each sampling plot and not recorded within the plot, which we term 'incidental species', were also identified and recorded on the data sheets. For incidental species in the understorey, only the number of individuals per species was recorded. All incidental species were included in the computation of species diversity for the area. Voucher specimens were also collected.

Properties of peat and water

Peat samples were collected to a depth of 30 cm using a split soil core sampler (AMS Inc., American Falls, ID, USA). One core (known volume) per plot was subsequently oven dried (65 °C for six days) and weighed to determine bulk density. Ten additional cores were collected randomly from each plot to assemble a composite sample weighing approximately 2 kg for laboratory determination of soil acidity (pH; potentiometric method), nitrogen (total N; Kjeldahl method), phosphorus (total P; Bray P2 method), potassium (total K; flame photometric method), organic carbon (TOC; Heanes wet oxidation) and organic matter (OM; Walkley-Black method).

One composite water sample per plant community type was assembled by scooping water from the holes created by collection of soil samples using a suitably sized plastic container. The volume of water collected was more than one litre for all communities except tall pole forest, where the depth of the water table limited the amount of water that could be extracted per scoop. In the laboratory, the water samples were analysed for pH (potentiometric method), nitrate (NO_3-N) and ammonium (NH_4-N) (steam distillation method), phosphate (PO_4) (vanadomolybdophosphoric acid or colorimetric method), total suspended solids (TSS) and total dissolved solids (TDS) (gravimetric methods).

All of the laboratory analyses were carried out, according to standard procedures, by technical staff at Central Mindanao University.

In all of the soil profiles we examined, it was possible to recognise a surface layer of peat 'soil' whose different appearance we attribute to its being permanently to occasionally above the water table (i.e. experiencing periodic air entry). For the purposes of this study, we equate this layer to the acrotelm (Ingram 1978). Acrotelm thickness and water table depth were determined by digging holes and measuring from the ground surface down to the base of the acrotelm and to the water table using a ruler. Measurements were also obtained using the ten holes from which the soil and water samples were collected. Thus, water table depths were recorded as positive values relative to the ground surface level, measured downwards from the surface. In cases where the water table was at or above the (flooded) surface, (negative) water table depth was again measured relative to (upwards from) the ground surface using a ruler.

The total thickness of the peat layer was assessed using a 10 m auger, whose length imposed a limit on the maximum peat layer thickness that could be recorded in this study.

Diversity indices and data analysis

Plot diversity indices (Shannon-Wiener H′, Simpson) were generated using open-source *BioDiversity Pro* software (McAleece *et al*. 1997). Correlation analyses of the data gathered on vegetation, peat and water chemistry were carried out to examine the associations between dependent biotic variables such as species richness (number of species, diversity indices) and vegetation structure (height, diameter), and twelve independent abiotic variables (water pH, NO_3-N, NH_4-N, PO_4, peat/soil pH, organic matter, total organic carbon, total nitrogen, total phosphorus, total potassium, acrotelm thickness and total thickness of peat). Non-metric multidimensional scaling (NMDS; in PAST (Øyvind *et al*. 2001)) and analysis of variance (ANOVA; SPSS 12) tests were used to further explore variation amongst the observed characteristics of the forest subtypes; the results of these analyses are summarised in the Appendix (Figures A1–A2 and Table A1).

RESULTS

Forest structure and species composition

Our analyses show distinct changes in forest structure and species composition on the eastern side of the peatland, from the fringing tall pole forest to the pygmy forest (Figure 2). The distinction of four zones in this sequence is strongly supported by ANOVA on the basis of stand structure (Table A1). Most of the tree species are common to all zones but vary between zones in height, diameter and relative abundance. Six habitat subtypes or plant communities (Figures 3 and 4) can be recognised on the basis of the apparent changes in structure and floristic composition, and these are described below.

(i) Tall pole forest

The tall pole forest is the ecosystem's fringing vegetation, which spans an area of about 3,124 ha and is located approximately 0.7–1.1 km west of the Gibong River. This forest subtype is composed of trees up to 30 m or more in height, generally in better-drained locations. It is the most species-rich forest subtype in the whole of the Caimpugan peatland area (H′ = 1.43). It is dominated by the distinctive *Tristaniopsis decorticata* and the stilt-rooted *Calophyllum sclerophyllum*, with the occasional presence of *Mangifera caesia*. Other common canopy-forming species with heights in the range 21–25 m include *Ardisia squamulosa*, *Baccaurea philippinensis*, *Teijsmanniodendron ahernianum*, *Engelhardtia serrata*, *Cryptocarya subvelutina*, *Ilex cymosa*, *Arthrophyllum ahernianum*, *Fagraea philippinensis* and *Palaquium tenuipetiolatum*. The shrub/small tree layer includes *Cleistanthus myrianthus*, *Mischocarpus triqueter*, *Drypetes monosperma*, *Garcinia vidalii*, *Cinnamomum burmanni* and *Psychotria diffusa*. The herb/fern layer is dominated by the ubiquitous spiny *Thoracostachyum sumatranum*, while *Stenochlaena palustris* is also abundant.

(*ii*) *Tall intermediate forest*

The physiognomy of this forest subtype is characterised by a gradual decrease in tree height and stem diameter, with dense stands dominated by

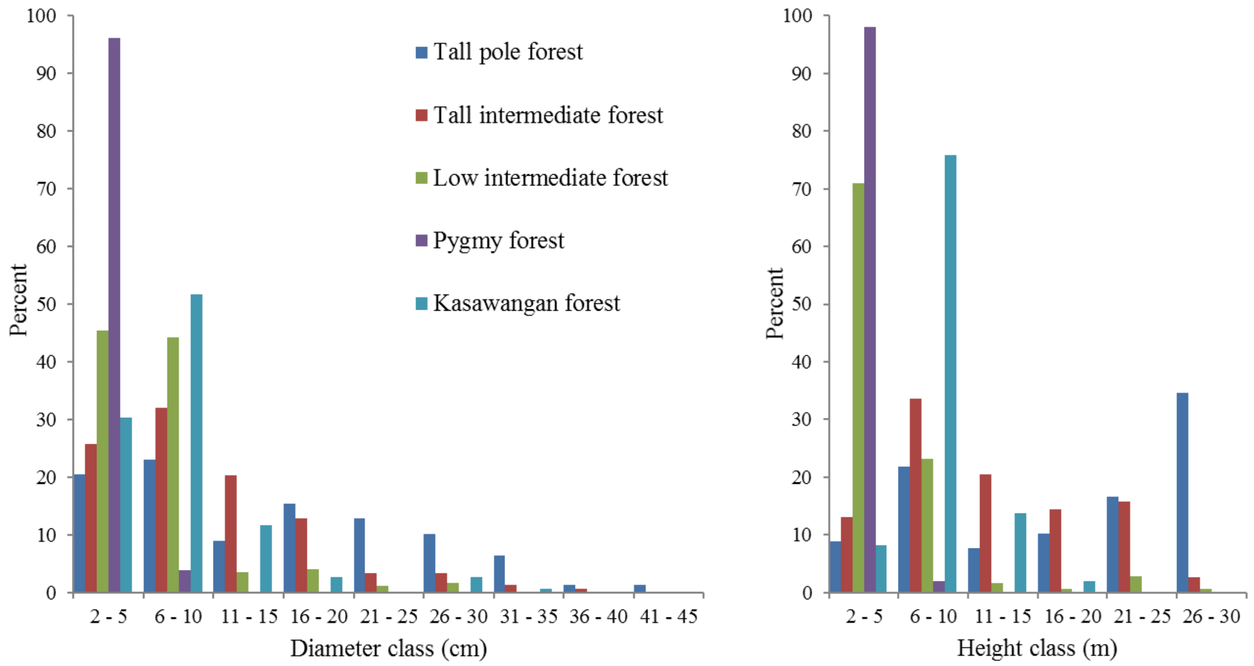

Figure 2. Left: tree DBH categories (percentage of trees with DBH ≥ 2 cm); right: tree height data (percentage of trees in each height category) in the different forest subtypes at Caimpugan.

Tristaniopsis decorticata. It is situated adjacent to the innermost stand of tall pole forest, 1.3–2.0 km west of the Gibong River, but can hardly be distinguished on satellite images. Generally, tree height varies from < 5 to 25 m, with some emergents reaching 26–30 m. The canopy-forming species include *Tristaniopsis decorticata*, *Calophyllum sclerophyllum* and *Ilex cymosa*. Other species in this canopy layer with heights ranging from 11 to 20 m are *Palaquium tenuipetiolatum*, *Cryptocarya subvelutina*, *Fagraea philippinensis* and *Arthrophyllum ahernianum.* The smaller trees include *Garcinia vidalii*, *Garcinia sulphurea*, *Kayea philippinensis*, *Baccaurea philippinensis*, *Macaranga leytensis*, *Syzygium tenuirame* and *Omphalea philippinensis*. The herb/fern layer of the intermediate forest is dominated by *Thoracostachyum sumatranum*, *Microsorum samarense* and *Stenochlaena palustris*.

(*iii*) *Low intermediate forest*

The low intermediate forest is characterised by an abrupt decrease in tree height and stem diameter (from the tall intermediate forest). Its canopy is dominated by *Tristaniopsis decorticata*, *Ilex cymosa* and *Arthrophyllum ahernianum*. The other notable tree species present include *Syzygium teniurame*, *Fagraea racemosa*, *Garcinia vidalii*, *Cinnamomum burmanni* and *Macaranga leytensis.* This forest subtype occurs in a narrow strip 2.1–2.3 km west of the Gibong River and occupies approximately 566 ha. Ninety percent of the trees sampled have a stem diameter range of 2–10 cm. For tree heights, 70 % of the trees are 2–5 m tall and > 20 % are placed in the 6–10 m height class (Figure 2). The herb/fern layer is dominated by *Thoracostachyum sumatranum* and includes *Stenochlaena palustris*, *Hanguana malayana*, *Calamus multinervis* and *Nepenthes mirabilis*.

(*iv*) *Pygmy forest*

The pygmy forest is a stunted formation located approximately 2.3–3.1 km west of the Gibong River. This is the forest subtype at the centre of the peatland which occupies an area up to 5.3 km wide, estimated to cover 1,101 ha. It is the forest zone with the lowest tree species diversity (H′ = 1.041). The peat layer is

Figure 3. Examples of three of the forest types distinguished at the Caimpugan peatland, namely: tall pole forest (top left), tall intermediate forest (right) and low intermediate forest (bottom left).

much thicker here, and the area is perennially inundated with water as indicated by the copious presence of *Sphagnum junghuhnianum* and other mosses creating mound-like formations. Only 2 % of the trees belong to the 6–10 m height class, while 98 % are less than 5 m tall, with no evident canopy stratification. *Tristaniopsis decorticata, Ilex cymosa* and *Arthrophyllum ahernianum* are the dominant species. In terms of stem diameter, 96 % of the trees belong to the 2–5 cm DBH class and only 4 % to the 6–10 cm class (Figure 2). In the herb/fern stratum, apart from the abundant presence of mosses (especially *Sphagnum junghuhnianum*), *Thoracostachyum sumatranum* and the stunted *Stenochlaena palustris* are common.

(*v*) *Kasawangan forest*

The Kasawangan forest is located in the western part of the peatland, approximately 4.2–4.35 km from the Gibong River and 0.62–3.5 km from the Agusan River. This forest occurs around the periphery of Lake Kasawangan, whose shores are mostly dominated by various sedge and grass species such as *Lepironia articulata, Fimbristylis globulosa* and *Isachne myositis,* among others. The Kasawangan forest exhibits differences in physiognomy and species composition when compared to the other forest subtypes. Forty-three percent of the trees belong to the 6–10 cm DBH class and only 3 % to the 26–30 cm class; also, 64 % of the trees are 6–10 m tall while only 2 % are 16–20 m tall. Species dominance varies from the typical *Tristaniopsis-Calophyllum* association and *Syzygium teniurame* dominates the plots. In terms of species composition, the species that we identified are: *Barringtonia acutangula* ssp. *acutangula, Cinnamomum burmanni, Cryptocarya mindanaensis, Cyptocarya subvelutina, Garcinia vidalii, Garcinia sulphurea, Ilex cymosa, Vatica odorata* spp. *mindanaensis, Litsea velutina, Melastoma malabathricum, Ternstroemia philippinensis, Syzygium teniurame* and two other species of *Syzygium*. The herb/fern layer is dominated by *Thoracostachyum sumatranum, Fimbristylis globulosa* and *Lepironia articulata*.

(*vi)* Lycopodium-Dicranopteris *plant community*

The *Lycopodium-Dicranopteris* plant community is chiefly dominated by fern species, with the occasional presence of tree seedlings. Fifteen species were identified within the two plots established, namely: *Alphitonia philippinensis, Arthrophyllum ahernianum, Bolbitis rhizophylla, Dicranopteris linearis, Fagraea racemosa, Isachne pulchella,*

Figure 4. Examples of three plant community types distinguished at the Caimpugan peatland, namely: pygmy forest (top left), Kasawangan forest (left) and the *Lycopodium-Dicranopteris* plant community (above).

Lycopodium pinifolium, Melastoma malabathricum, Melicope triphylla, Scleria scrobiculata, Stenochlaena palustris, Syzygium teniurame, Ternstroemia philippinensis and *Thoracostachyum sumatranum*, along with a few mature trees and seedlings of *Musanga cecropioides* (an exotic species) that were observed along the edge of the plant community. The *Lycopodium-Dicranopteris* plant community may be regarded as a distinctive occurrence in the Caimpugan peat swamp forest. The two sites sampled cover approximately 2 ha. The first site is located in the low intermediate forest at 8° 23′ 40.26" N, 125° 53′ 35.18" E; and the second lies within the pygmy forest at 8° 23′ 44.84" N, 125° 53′ 42.90" E. Smaller patches of this community occur elsewhere within the peatland.

Peat chemistry

The bulk density of the upper 30 cm layer of the peat observed in this study ranged from 0.36 g cm^{-3} to 0.83 g cm^{-3} with a mean of 0.61 g cm^{-3}. The average pH level for all plots was 3.6 (Figure 5), which could be classified as very strongly acidic (Horneck *et al.* 2011). The phosphorus and potassium levels are classified as high, with average values of 659 ppm and 415 ppm (dry weight basis), respectively (Figure 5). A positive correlation ($r = 0.649$, $n = 12$, $P < 0.05$) was observed between plant diversity and peat organic matter, while no significant correlations were found between the other variables. Recognition of the four vegetation zones was strongly supported by NMDS on the basis of peat chemistry (Figure A1).

Water table, acrotelm and peat thickness

Data on water table depth plus acrotelm and peat thickness are presented in Table 1. Among the four vegetation zones at the eastern side of the peatland, the tall pole forest had the lowest water table levels, while the water table was above or near the surface of the acrotelm in all other zones. A strong negative correlation was observed between peat thickness and the structure of vegetation (i.e. the height and

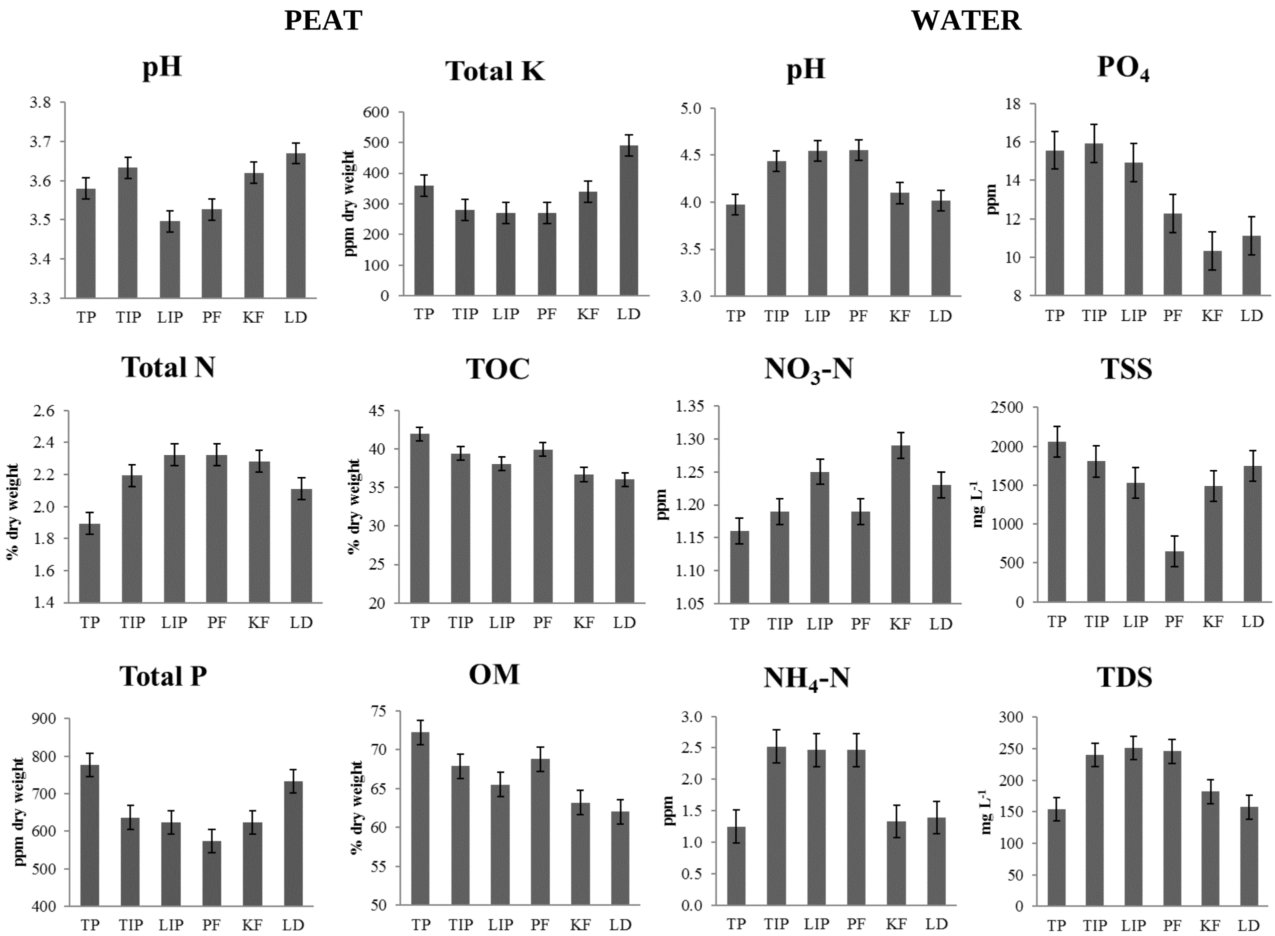

Figure 5. Chemical properties of peat and water in the six forest types/plant communities at Caimpugnan: TP = tall pole, TIF = tall intermediate, LIF = low intermediate, PF = pygmy and KF = Kasawangan forest; LD = *Lycopodium-Dicranopteris* community. TOC = total organic carbon; OM = organic matter; TSS = total suspended solids; TDS = total dissolved solids. The error bars indicate ± SE.

diameter of trees; r = -0.650, n = 12, P < 0.05 in both cases). Similarly, the number of individuals was highly negatively correlated (r = -0.860, n = 12, P < 0.01) with acrotelm thickness, while in contrast the height and diameter of trees were both highly positively correlated (r = 0.887 and r = 0.865, respectively; n = 12 and P < 0.01 in both cases) with acrotelm thickness. All other variables showed no significant correlation with forest structure.

Species diversity and composition

Generally, higher species diversity was observed in the tall pole forest than in any other zone of the peat swamp forest (Figure 6). Analysis of variance showed highly significant differences in species diversity between and among the forest subtypes (Table A1). Moreover, *Tristaniopsis decorticata*, *Thoracostachyum sumatranum*, *Syzygium tenuirame*, *Calophyllum sclerophyllum*, *Stenochlaena palustris*, and *Sphagnum junghuhnianum* - identified as outliers by the NMDS analysis - can be regarded as the most important species in driving differences between the forest subtypes (Figure A2). Plot 2 in the tall pole forest had the highest Shannon-Weiner diversity index, whereas Plot 1 of the *Lycopodium-Dicranopteris* plant community had the highest Shannon evenness (J) value. The three highest Simpson's reciprocal index (1/D) values were obtained for the plots in tall pole forest. The properties of this index are such that the higher the value, the greater the diversity, and the maximum value is the number of species. Since all values exceeded unity, all of the individuals in the plots belonged to different species.

Table 1. Physical characteristics of peat and water table in the different forest subtypes of the Caimpugan peat swamp forest. Negative water table depth measurements indicate the depth of flooding of the ground surface.

Vegetation zone	Plot	Acrotelm thickness (cm)	Peat thickness (m)	Water table depth (cm)
Tall pole forest	1	15.80	9.85	15.83
	2	16.00	10.00	16.05
	3	16.76	7.25	16.79
Tall intermediate forest	1	13.59	> 10.00	-1.58
	2	14.20	> 10.00	-1.61
	3	15.49	> 10.00	-1.45
Low intermediate forest	1	10.16	> 10.00	-2.10
	2	8.26	> 10.00	-2.12
	3	10.76	> 10.00	-2.09
Pygmy forest	1	6.73	> 10.00	-29.18
	2	7.87	> 10.00	-31.57
	3	8.00	> 10.00	-33.53
Kasawangan forest	1	9.39	> 10.00	-2.94
	2	3.81	4.90	-3.83
	3	10.16	10.00	-10.20
	4	10.67	> 10.00	-10.68
Lycopodium - Dicranopteris	1	10.92	> 10.00	-10.93
	2	10.85	> 10.00	-10.86

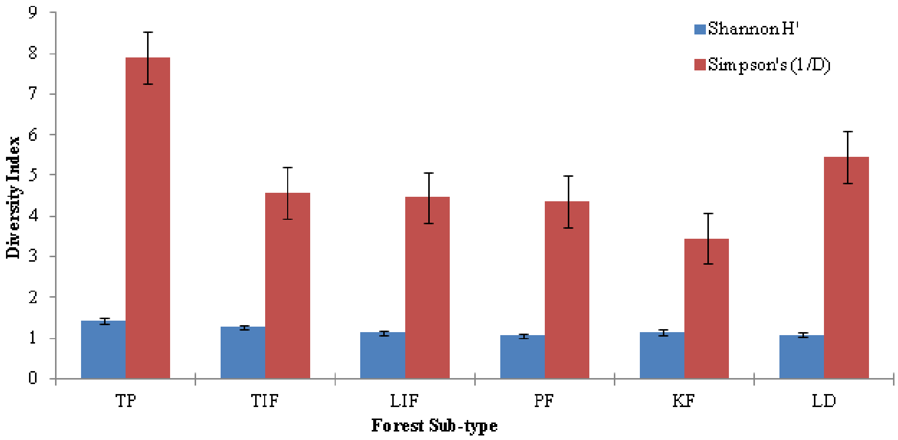

Figure 6. Diversity indices for all of the plant communities studied in the Caimpugan peat swamp forest. The plant communities are: tall pole forest (TP), tall intermediate forest (TIF), low intermediate forest (LIF), pygmy forest (PF), Kasawangan forest (KF) and *Lycopodium-Dicranopteris* community (LD). The error bars indicate ± SE.

DISCUSSION

Species diversity and composition

In total, 101 vascular plant species belonging to 56 families and 81 genera were recorded amongst the trees and understorey vegetation of the 18 plots established in the Caimpugan peat swamp forest, as reported by Aribal & Fernando (2014). The species diversity observed in this study is similar to that reported from other studies in the peat swamp forests of Southeast Asia (Table 2). Posa *et al.* (2011) estimate the total number of plant species in Southeast Asian peat swamp forests at 1,524, of which only 172 are restricted to or strongly associated with peat swamp forest.

The families represented by tree species at Caimpugan include Anacardiaceae, Annonaceae, Aquifoliaceae, Araliaceae, Clusiaceae, Dipterocarpaceae, Euphorbiaceae, Fabaceae, Gentianaceae, Juglandaceae, Lamiaceae, Lauraceae, Lecythidaceae, Melastomataceae, Myrsinaceae, Myrtaceae, Putranjivaceae, Rubiaceae, Sapindaceae Sapotaceae, Symplocaceae and Theaceae. The tree flora of this site is similar in terms of family and species composition to the peat swamp forest flora of Sarawak and Brunei catalogued by Anderson (1963). However, the families Putranjivaceae (represented by the genus *Drypetes*) and Juglandaceae (*Engelhardtia*) are not amongst the list of families reported by Anderson (Aribal & Fernando 2014). Plant families found in Caimpugan that commonly occur in peat swamp forest in Southeast Asia include Anacardiaceae, Annonaceae, Burseraceae, Clusiaceae, Dipterocarpaceae, Euphorbiaceae, Lauraceae, Leguminosae, Myristicaceae, Myrtaceae and Rubiaceae (Wyatt-Smith 1959, Morley 1981, Bruenig 1990, Ibrahim & Hall 1992, Shepherd *et al.* 1997). On the other hand, no representatives of the families Bombacaceae (= Malvaceae), Burseraceae and Myristicaceae have so far been found at Caimpugan. Moreover, the Dipterocarpaceae are represented solely by *Vatica odorata* ssp. *mindanaensis* at Caimpugan, compared to six species reported by Page *et al.* (1999), four by Mogea & Mansur (2000), 12 by Simbolon & Mirmanto (2000) and six by Siregar & Sambas (2000), from various peat swamp forests in Southeast Asia.

The most diverse vegetation zone of the Caimpugan peatland is the tall pole forest, and the least diverse is the pygmy forest. Page *et al.* (1999) emphasise that the most important limiting factors for the floral diversity and structure of peat swamp forest are the hydrology and nutrient status of the peat, which determine the condition of the forest that can grow upon it. In line with this, pygmy forest has lower solute levels and lower diversity indices than the other forest subtypes at Caimpugan. Species dominance varies significantly amongst Southeast Asian peat swamp forests. For instance, Mirmanto (2010) identified *Combretocarpus rotundatus*, *Palaquium leiocarpum*, *Stemonurus scorpioides* and *Tristaniopsis whiteana* as the dominant species of the Sebangau peat swamp forest in Central Kalimantan (Indonesia), whereas Siregar & Sambas (2000) enumerated the most abundant trees in peat swamp forest in West Kalimantan as *Blumeodendron elateriospermum*, *Cyathocalyx biovulatus*, *Blumeodendron tokbrai*, *Lithocarpus encleisocarpus* and *Syzygium chloranthum*. In terms of abundance (number of individuals), *Tristaniopsis decorticata* is

Table 2. Comparison of the diversity of trees and other vascular plants reported from peat swamp forests in Southeast Asia. All except the last two sites listed are in Indonesia. NP = National Park.

Location	Number of taxa	Area sampled (ha)	Reference
Riau province, Sumatra	78, 75, and 68 species in three sampling plots	0.60	Mogea & Mansur (2000)
Suaq Balimbing, South Aceh	44 species, 35 genera, 25 families	1.6	Purwaningsih (2000)
Sebangau, Central Kalimantan	215 species	3.0	Husson *et al.* (2018)
Sebangau, Central Kalimantan	100 species	1.35	Page *et al.* (1999)
Tanjung Puting NP and Sebangau, Central Kalimantan	310 species, 78 families	0.20	Simbolon & Mirmanto (2000)
Giam Siak Kecil–Bukit Batu Biosphere Reserve, Sumatra	135 species, 34 families	3.00	Gunawan *et al.* (2012)
Pahang, Malaysia	287 species, 52 families	0.50	Hassan *et al.* (2007)
Caimpugan, Mindanao, Philippines	101 species, 81 genera, 56 families	0.17	This study

the dominant tree species of the Caimpugan peat swamp forest, which thus resembles peat swamp forest on Sumatra and in eastern Borneo where the genus *Tristaniopsis* has greater dominance according to Whitmore (1984). The same observation was made by Polak (1975) in relation to peat swamp forest on the Panch Peninsula of Sumatra, where the central zone is a low, open woodland dominated by a species of *Tristaniopsis.* Although *Tristaniopsis* species occur in the central parts of some peat swamp forests, they are more generally typical of *kerapah* (permanently waterlogged heath) forests on deep peat between 0 and 1200 m a.s.l. Examples can be found in basins on Pueh Forest Reserve in West Sarawak, as well as in the Bionio River Basin and on the Merurong Plateau in central Sarawak (Bruenig 1974).

Variation in forest vegetation and structure

The distinction of four vegetation zones west of Gibong River is strongly supported by ANOVA on the basis of stand structure (diameters and heights of trees), as well by as ordination analysis via NMDS on the basis of peat chemistry. The ANOVA results for crown structure also explain the similarity between tall pole forest and tall intermediate forest, which are indistinguishable on satellite images. Furthermore, NMDS depicted the pattern of clustering among the plots of the four forest subtypes, with those situated close to each other exhibiting similarities in terms of stand structure and peat properties.

The sequence of variation in forest characteristics at Caimpugan commences with the most diverse tall pole forest, followed by the dense tall intermediate forest then the low intermediate forest, and ends with the stunted pygmy forest in the centre of the peatland. The tall pole forest identified in this study may be broadly equivalent to the ‘mixed swamp forest’ recognised by Anderson (1964) and Page *et al.* (1999). There are commonalities, such as: (i) the forest is tall and stratified with an upper canopy at 35 m, a closed layer at 15–25 m and a more open layer of smaller trees 7–12 m in height; and (ii) many of the trees have stilt or buttress roots and pneumatophores are frequent. Similarly, the tall intermediate forest may be comparable to the ‘transition forest’ described by Page *et al.* (1999) in terms of the following shared characteristics: (i) the upper and middle canopies are composed of a range of species similar to those of mixed swamp forest (or the equivalent tall pole forest) although the species densities are greater; and (ii) the forest canopy reaches a maximum height of 25–30 m and few trees develop buttresses or stilt roots. This subtype, as recognised here, differs from the ‘intermediate forest' of Davies (2006), which we consider to be low intermediate forest; although the Caimpugan low intermediate forest has no equivalents in the classifications of Anderson (1963) and Page *et al.* (1999). Our pygmy forest is comparable to the ‘very low canopy forest' described by Page *et al.* (1999), on the basis of common attributes which include: (i) the area has permanently high water table and is characterised by large pools interspersed with forest-covered islands; (ii) few of the trees are more than 1.5 m tall; (iii) there is high coverage of bryophytes on the peat surface; and (iv) the spiny sedge *Thoracostachyum sumatranum* is the most frequent vascular plant on the forest floor.

There is a trend of increasing number of trees per plot through the whole sequence of forest subtypes studied in Caimpugan. This was also observed by Page *et al.* (1999) in Sebangau, with the exception of their tall pole forest. Moreover, the sequence of change observed is similar to that described by Anderson (1963) in Malaysia and by Bruenig (1990) on Sumatra and Borneo. The change in forest structure at Caimpugan appears to be associated with variations in peat thickness; a suggestion supported by the observations of Morley (1981) and Page *et al.* (1999). In the Caimpugan peat swamp forest, the tall pole forest located closer to the river has lower water table and shallower peat; and as peat thickness increases and permanently high water table conditions develop through the sequence of forest subtypes, there is a concomitant decrease in the heights and diameters of trees. According to Anderson (1963) there is a continuum of change in forest structure from the uneven-canopied tall forest near the edge of the swamp through zones of lower tree height, decreased girth, thicker leaves and lower species richness, towards its centre.

Interdependence of vegetation and peat properties

Peat thickness, acrotelm thickness and vegetation

Variations in peat thickness and vegetation structure were positively correlated in this study. In the Caimpugan peatland, the tall pole forest is situated on shallower peat while the tall intermediate forest, low intermediate forest and pygmy forest occur on deeper peat, based on averages of measurements. On the other hand, the tall pole forest has a thicker acrotelm and lower water table than the other forest subtypes. This general pattern in vegetation structure relative to peat thickness has been observed in almost all of the peat swamp forests in Southeast Asia (Bruenig 1990). Ingram (1967) and Sparling (1967) explain that vegetation near the periphery of a peat dome receives an increased water flow and, consequently, an increased rate of supply of solutes and dissolved oxygen.

As recognised previously by Anderson (1983) and Page *et al.* (1999), the heights and diameters of trees decrease as the thickness of peat increases. However, this may not always be the case. For instance, Page *et al.* (1999) discovered tall interior forest in the Sebangau catchment. The occurrence of the tallest forest on the thickest peat at Sebangau is surprising since it was believed previously that peat more than 3 m thick could support only low pole forest (Sieffermann *et al.* 1988). Bruenig (1990) stated that there is a general trend of change along the successional gradient (i.e. with increasing peat thickness) in attributes such as canopy height, crown size and grouping of crowns, as well as in the basal areas of the most important timber species and species groups; and that this trend is consistent throughout the region - indeed, it is so regular that it can be used to classify the forests into types for forest inventories.

We also noted that there were fewer individuals per unit area in locations with thicker acrotelm. In the Caimpugan peatland, the tall pole forest (situated in areas with thicker acrotelm) has larger but more sparsely distributed trees; moving through the tall intermediate and low intermediate forest to the pygmy forest at the centre of the peatland, the vegetation tends to become denser with slender boles, and this is associated with decreasing acrotelm thickness.

Peat chemistry

The peat bulk densities observed in this study are slightly higher than the values observed by Lambert & Staelens (1993) and Sajarwan *et al.* (2002), which varied between 0.12 and 0.17 g cm^{-3} for undisturbed peat swamp forest. The highest value (0.833 g cm^{-3}) recorded in this study was observed at the sampling plots in Kasawangan forest and we suggest this can be attributed to disturbance arising from the hunting and fishing activities of local people. The range of pH observed in this study was approximately the same as the ranges reported by Sayok *et al.* (2008) in Loagan Bunut National Park (Sarawak) and by Page *et al.* (1999) at Sebangau (Central Kalimantan). The average nitrogen level of 2.08 ± 0.47 % observed in this study is slightly higher than that reported by Page *et al.* (1999), which ranged from 0.8 to 1.9 %. The phosphorus level, at 659.44 ± 181.33 ppm, is higher than reported by Salemin *et al.* (2010) (219.20 ± 18.79 ppm) and Page *et al.* (1999) (125.86 ± 6.41 ppm). For potassium in the 0–30 cm peat layer, the range of values we observed (415 ± 159.24 ppm) is similar to that found by Page *et al.* (1999).

Tree height, tree diameter and acrotelm thickness

The tall pole forest, with its thicker acrotelm, possesses larger diameter and taller trees than the pygmy forest, which has a thinner acrotelm and stunted trees of small diameter. This pattern is similar to the findings of Page *et al.* (1999) at Sebangau (Central Kalimantan). According to these authors, the movement of water across the peatland dome must be considered because this water flow brings with it a constant supply of nutrients in low concentration that the trees can use for their growth. The mixed swamp forest of Page *et al*. (1999) (equivalent to the tall pole forest in this study) and the riverine forest zone are the final recipients of all the water flowing from the interior of the peatland and this may, in part, explain the greater height and girth of the canopy trees in these parts of the Caimpugan peatland, compared to the low pole and pygmy forest subtypes. However, the roots of trees in the tall pole forest may also penetrate beneath the shallow peat layer and thus derive additional solutes from the underlying mineral soil.

CONCLUSIONS

As one of the first such studies in the Philippines, the results and generalisations presented here provide a first foundation for management of the unique and important, yet under-studied, wetland forest ecosystem at Caimpugan. The variations we have observed in vegetation structure suggest that it is interdependent with peat thickness and associated with the physical, chemical and hydrological conditions of the peat. It is also recognised that the spatial patterns in peat accumulation, the vegetation diversity and the structure of the forest are concomitant with hydrology and solute availability, although the variation in forest vegetation and/or species composition cannot be causatively attributed to the chemical properties of either the peat or the peat water. Furthermore, we believe that this study supports the notion that the interdependence between the forest and the peat, along with its vital ecological functions, operates only within the very sensitive and superficial layer known as the acrotelm since, though relatively shallow, the acrotelm is the layer where decomposition of organic material occurs and the eventual source of the slow but constant release of solutes that facilitates plant growth. This further implies that, for the peat swamp forest and/or peatland to function effectively as a carbon sink and regulator of water flow so as to minimise flood peaks, the forest vegetation must be protected and conservation efforts should focus on retaining it, since the vegetation is crucial for the peatland ecosystem's integrity. It follows from the interrelations between vegetation and peat hydrology that conserving or restoring the natural flooded hydrological conditions is also of critical importance for conserving this ecosystem.

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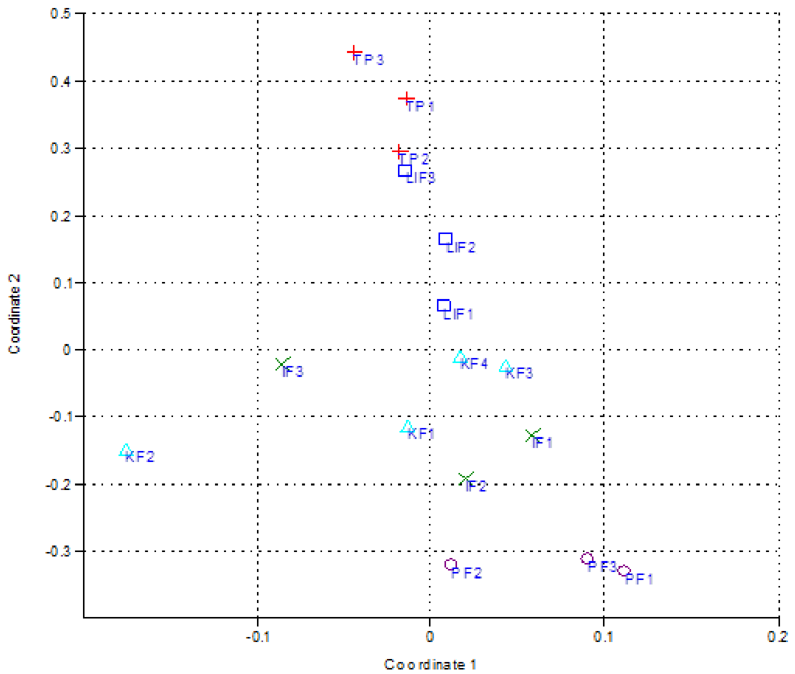
Appendix: Results of statistical analyses



Key to forest subtypes

TP: tall pole forest
(red vertical crosses)

IF: tall intermediate forest
(green diagonal crosses)

LIF: low intermediate forest
(dark blue squares)

PF: pygmy forest
(red circles)

KF: Kasawangan forest
(light blue triangles)

Figure A1. Non-metric multidimensional scaling (NMDS) results comparing forest subtype characteristics (tree diameter, tree height, number of species) with peat properties (listed in Table A1). The letters in each data-point label refer to a forest subtype (see key) and these are appended with the plot number.

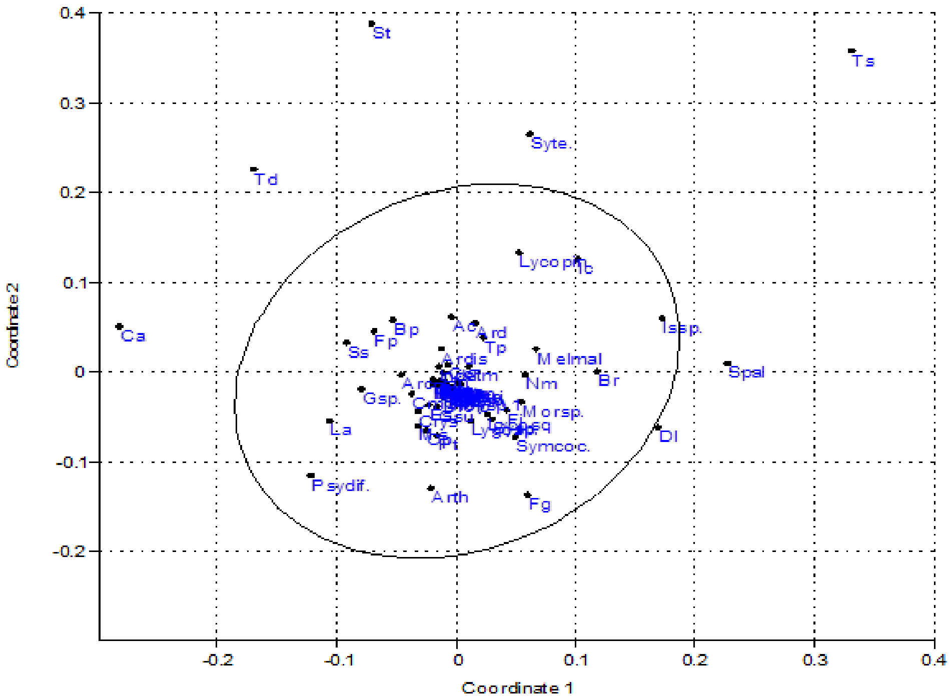


Figure A2. Non metric multidimensional scaling (NMDS) on species community trends in the Caimpugan peat swamp forest. The seven species falling outside the circle are the most important for delineating differences between the forest subtypes (Ca = *Calophyllum sclerophyllum*, Dl = *Dicranopteris linearis*, Spal = *Stenochlaena palustris*, St = *Sphagnum junghuhnianum*; Syte = *Syzygium tenuirame*; Td = *Tristaniopsis decorticata*; Ts = *Thoracostachyum sumatranum*. Abbreviations for the 103 species falling within the circle are not provided to save space; all species are listed by Aribal & Fernando (2014).

Table A1. Analysis of variance (ANOVA) on the stand structure (DBH = diameter at breast height), diversity index, water properties (TSS = total suspended solids; TDS = total dissolved solids) and peat physical and chemical properties (TOC = total organic carbon; OM = organic matter) of the six forest subtypes distinguished in the Caimpugan peat swamp forest.

Variable	F[1]	Tall pole forest[2]	Tall intermediate forest[2]	Low intermediate forest[2]	Pygmy forest[2]	Kasawangan forest[2]	*Lycopodium-Dicranopteris*[2]
Stand structure							
DBH (cm)	108.85**	19.31 (6.75)^{a}	12.83 (6.08)^{b}	7.65 (4.73)^{c}	2.69 (1.09)^{d}	8.27 (5.12)^{c}	n/a
Mean height (m)	289.54**	25.64 (7.94)^{a}	15.16 (6.29)^{b}	5.95 (3.9)^{d}	2.91 (0.89)^{e}	8.63 (2.33)^{c}	n/a
Crown diameter (m)	86.78**	2.22 (0.9)^{a}	1.97 (1.06)^{ab}	1.73 (0.95)^{b}	0.5 (0.22)^{c}	0.73 (0.74)^{c}	n/a
Basal area (m^2)	53.53**	0.03 (0.02)^{a}	0.02 (0.01)^{b}	0.01 (0.01)^{c}	0 (0)^{d}	0.01 (0.01)^{c}	n/a
Diversity indices							
Shannon H'	12.12**	1.43 (0.06)^{a}	1.28 (0.11)^{ab}	1.13 (0.1)^{bc}	1.07 (0.02)^{c}	1.15 (0.04)^{bc}	1.08 (0.05)^{c}
Simpson	5.93**	7.9 (0.37)^{a}	4.57 (2.15)^{b}	4.46 (1.11)^{b}	4.36 (0.68)^{b}	3.46 (0.49)^{b}	5.47 (1.27)^{ab}
Water properties							
pH	1.34^{ns}	3.98 (0.07)	4.56 (0.78)	4.02 (0.04)	4.04 (0.1)	4.07 (0.06)	4.18 (0.08)
NO_3-N (ppm)	0.89^{ns}	1.16 (0.1)	1.19 (0.14)	2.23 (2.06)	1.16 (0.1)	1.07 (0.11)	0.96 (0)
NH_4-N (ppm)	0.84^{ns}	1.25 (0.05)	2.46 (2.31)	1.39 (0.3)	1.36 (0.28)	1.07 (0.15)	1.27 (0.06)
PO_4 (ppm)	3.46*	15.57 (1.71)^{a}	12.27 (3.7)^{ab}	11.13 (2.09)^{ab}	9.32 (0.55)^{ab}	10.86 (2.73)^{ab}	7.88 (0.39)^{b}
TSS (mg L^{-1})	0.84^{ns}	2057 (1100.21)	646 (76.37)	1745.33(1321.62)	1565.33(1304.79)	1451.25(1497.15)	343 (282.84)
TDS (mg L^{-1})	1.92^{ns}	154 (36.39)	246 (110.49)	157.33 (21.01)	163.33 (28.02)	143 (21.32)	129 (1.41)
Physical and chemical properties of peat							
Bulk density (g m^{-3})	0.53^{ns}	0.57 (0.13)	0.69 (0.09)	0.65 (0.03)	0.58 (0.14)	0.62 (0.22)	0.49 (0.18)
TOC (% dry wt.)	0.40^{ns}	41.98 (5.38)	39.99 (1.91)	39.33 (11.65)	42.85 (1.9)	38.22 (7.63)	35.45 (5.29)
Total N (mg L^{-1})	1.36^{ns}	1.89 (0.22)	2.32 (0.33)	2.15 (0.25)	2.5 (0.57)	1.73 (0.48)	2 (0.8)
Total P (mg L^{-1})	1.18^{ns}	0.08 (0.02)	0.06 (0.01)	0.08 (0.01)	0.05 (0.01)	0.07 (0.03)	0.05 (0.01)
Total K (mg L^{-1})	2.05^{ns}	0.04 (0.01)	0.03 (0.01)	0.05 (0.02)	0.04 (0)	0.06 (0.02)	0.03 (0.01)
pH	0.60^{ns}	3.58 (0.15)	3.53 (0.17)	3.56 (0.36)	3.62 (0.06)	3.77 (0.2)	3.62 (0.23)
OM (%)	0.40^{ns}	72.21 (9.26)	68.78 (3.28)	67.65 (20.04)	73.7 (3.28)	65.74 (13.12)	60.97 (9.1)

[1] Values represent F statistics; df = 316 in all cases; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ^{ns} = not significant.

[2] Values are means (standard deviations in parentheses); different superscripted letters denote groups that differ significantly from each other in Tukey's HSD tests.