Habitat differentiation of obligate ultramafic Nepenthes endemic to Mount Kinabalu and Mount Tambuyukon (Sabah…

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Habitat differentiation of obligate ultramafic *Nepenthes* endemic to Mount Kinabalu and Mount Tambuyukon (Sabah, Malaysia)

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Abstract Localized ultramafic outcrops in Kinabalu Park (encompassing Mount Kinabalu and Mount Tambuyukon) in Sabah (Malaysia) are known for high levels of plant diversity and endemism, which have been stimulated by extreme soil chemistry and biogeographic factors, such as isolation. Characteristic of these outcrops are edaphic endemics of insectivorous pitcher plants from the *Nepenthaceae*-family including *Nepenthes burbidgeae, N. edwardsiana, N. macrovulgaris, N. rajah* and *N. villosa,* all of which (except *N. macrovulgaris*) are confined solely to the protected area of Kinabalu Park. Although the various aspects of plant taxonomy and nutrition of this genus have been extensively studied, the habitat of these rare species has to date not been studied in detail. It was hypothesized that while the *Nepenthes* of Mount Kinabalu and Mount Tambuyukon are excluders of excess trace elements, soil chemistry is nevertheless a major driver for creating the specific habitats in which ultramafic edaphic endemic *Nepenthes* occur, and that this is reflected in vegetation physiognomy and co-occurring species composition as well as in the foliar chemistry of *Nepenthes*. The results show that the characteristics of the physical environment and soil chemistry 'induces' a vegetation physiognomy that varies among sites and produces a series of different niches that are colonised by different *Nepenthes*-species. Although other plant species associated with these niches do not directly influence the distributions of the *Nepenthes*-species, some are characteristic. The unusual ultramafic soil chemistry is not reflected in the foliar chemistry of *Nepenthes* and they appear to be 'Excluders' of potentially toxic soil trace element concentrations. The populations of *Nepenthes burbidgeae, N. edwardsiana, N, rajah, N. villosa* are small (in particular, *N. burbidgeae*) and these species are thus likely to be vulnerable to the potential effects of climate change-induced drought and fire.

Communicated by Thomas Abeli.

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Introduction

Ultramafic soils, which are derived from minerals rich in magnesium, iron and nickel (Brooks 1987), are

widespread throughout Southeast Asia, but have a patchy distribution. The greatest expanses of ultramafic bedrock occur in northern Borneo (Sabah), the southern Philippines and parts of Wallacea and are prominent features of the landscapes of Sabah, Mindanao, Palawan, Halmahera and Sulawesi. The flora of ultramafic soils is often characterized by distinct species assemblages that are a consequence of extreme soil conditions (which include nutrient deficiency and high magnesium:calcium quotients) and biogeographic processes, in particular, vicariance (Brooks 1987; Proctor 2003). As such, it has been proposed that discrete ultramafic outcrops in conjunction with altitude (climatic conditions) may have stimulated the evolution of localized edaphic endemics (Beaman and Beaman 1990). Such 'edaphic endemics' (or ultramafic obligate species) are comparatively rare, and the great majority of plants that colonise ultramafic soils occur facultatively on such soils. Some plant species might not occur on ultramafic soils as a result of competitive exclusion by plant species that are highly specialized to grow under strong edaphic stress, and in turn ultramafic obligate species do not occur on other soils because of inherent slow growth rates and are thus outcompeted (Kazakou et al. 2008).

Carnivory in plants is a rare trait known from less than 600 species globally; the majority are in the angiosperm orders Caryophyllales and Lamiales. The carnivorous syndrome confers maximum benefits in habitats that constrain the acquisition of essential nutrients (N, P, K) from the soil, either because the nutrients are absent, or inaccessible. These conditions provide a competitive advantage to carnivorous plants, which are able to obtain supplementary nutrients through the capture and digestion of animals. Givnish et al. (1984) noted that in addition to low nutrients status, such habitats are often permanently wet and generally have high insolation. Carnivorous plants benefit from high levels of moisture because they tend to be poor at limiting water loss through the surfaces of their traps (Juniper et al. 1989). Overall, it has been shown that carnivorous plants have lower photosynthetic capacity compared with non-carnivorous plants (Ellison and Farnsworth 2005; Ellison 2006).

The monotypic Nepenthaceae is one of the largest carnivorous plant families, containing 138 species distributed in the Paleo-tropics ranging from Madagascar to New Caledonia (McPherson 2011), with centres of diversity in Borneo (34 species, 24 endemic)

and Sumatra (35 species, 25 endemic). *Nepenthes* is associated with ultramafic substrates throughout much of its range in Southeast Asia, suggesting that these soils somehow provide an optimal environment for the carnivorous syndrome. Whether this is driven directly by the chemistry of the soil itself, or indirectly by its effects on the physiognomy of the plant communities in which *Nepenthes* grow, has yet to be established. Ultramafic soils have high concentrations of trace elements (Ni, Co, Cr, Mn) that may be reflected in the foliar chemistry of plants that grow in them (Reeves 2003).

Nepenthes is a conspicuous component of the flora of ultramafic soils in Kinabalu Park. Spectacular species such as *Nepenthes rajah*, *N. burbidgeae*, *N. edwardsiana* and *N. villosa* are endemic to Mount Kinabalu and nearby Mount Tambuyukon, the two major mountains within the boundaries of Kinabalu Park. In accordance with the predictions of Givnish et al. (1984), the distribution of *Nepenthes* on Mount Kinabalu and Mount Tambuyukon indicates that they are abundant in vegetation that tends to be low, open and stunted (Clarke 1997). If the existence of open habitats with high insolation is *sine qua non* for *Nepenthes* (under concomitant permanently wet conditions) then it seems likely that the intrinsic high light requirement of the genus is facilitated by vegetation physiognomy rather than plant community composition or soil chemistry, but this has yet to be investigated.

In this study, we investigated the auto-ecological relationships between several *Nepenthes*-species and natural hybrids (viz. the species: *N. burbidgeae*, *N. edwardsiana*, *N. rajah*, *N. villosa* and the natural hybrids: *Nepenthes rajah × fusca*, *Nepenthes rajah × lowii*, *Nepenthes rajah × tentaculata*, *Nepenthes × alisaputrana* and *Nepenthes × kinabaluensis*) that are endemic to Kinabalu Park and co-occurring plant species and soil chemistry (Table 1). As these species are primarily edaphic endemics, they are contrasted with two other species (*N. macrophylla*, *N. lowii* and *Nepenthes × trusmadiensis*) that grow at comparable altitudes on nearby Mount Trus Madi, where ultramafic soils are absent. The former, *N. macrophylla,* is endemic to Mount Trus Madi, whereas *N. lowii* is more widespread in Sabah and Sarawak. We hypothesized that while the *Nepenthes* of Mount Kinabalu and Mount Tambuyukon are excluders of excess trace elements, soil chemistry is nevertheless a major driver for creating the specific habitats in which ultramafic edaphic endemic *Nepenthes* occur, and

Table 1 *Nepenthes*-species of Mount Kinabalu Park with general geological and altitudinal occurrence and distribution

Species	Habitat	Altitude (m asl)	Distribution
Nepenthes rajah	Terrestrial of graminoid scrub on ultramafic soil	1500–2570	Endemic to Mt Kinabalu & Mt Tambuyukon
Nepenthes villosa	Terrestrial of sub-alpine scrub on ultramafic soil	1800–3000	Endemic to Mt Kinabalu & Mt Tambuyukon
Nepenthes edwardsiana	Epiphyte of upper montane forest on ultramafic soil	1500–2600	Endemic to Mt Kinabalu & Mt Tambuyukon
Nepenthes burbidgeae	Terrestrial of stunted vegetation on ultramafic soil	1400–1900	Endemic to Mt Kinabalu & Mt Tambuyukon
Nepenthes macrophylla	Terrestrial or epiphyte in upper montane forest on sandstone soil	2000–2640	Endemic to Mt Trus Madi
Nepenthes lowii	Terrestrial or epiphyte in lower montane forest on ultramafic and non-ultramafic soils	1200–2640	Sabah and Sarawak

that this is reflected in vegetation physiognomy and co-occurring species composition as well as in the foliar chemistry of *Nepenthes*. Specifically, it was hypothesized that (1) vegetation physiognomy (mean height and tree density) determines habitat differentiation of *Nepenthes*-species; (2) co-occurring species can also be used to predict the occurrence of different *Nepenthes*-species; and (3) the unusual ultramafic soil chemistry is reflected in the foliar chemistry of *Nepenthes*.

Materials and methods

Study area

Kinabalu Park is located in the northern part of Sabah (Malaysia) on the island of Borneo and covers 754 km^2 (Fig. 1). The Park features two main mountains—Mount Kinabalu (4095 m) and Mount Tambuyukon (2579 m asl). Kinabalu Park has a humid tropical climate with a mean air temperature of 20 °C throughout the year at 1680 m asl (and a mean daily temperature of 12.6 °C at 2700 m asl) and mean annual rainfall of approximately 3000 mm with little altitudinal variation (Kitayama et al. 1999). Figure 2 provides an overview of the distribution of *Nepenthes* on Mount Kinabalu and Mount Tambuyukon and the plot localities (each distribution record equals a plot).

To contrast the habitat, soil and foliar chemistry of the ultramafic endemic *Nepenthes*-species with a non-ultramafic analogue, fieldwork also took place on Mount Trus Madi, which lies approximately 70 km south of Kinabalu Park and at 2642 m asl is the second highest mountain in Borneo. The entire range in which Mount Trus Madi lies is approximately 80 km long and the geology consists of the Trus Madi Formation of mudstone, shale and argillite with beds of quartzite, sandstone, siltstone and limestone breccias (Acres 1972).

Plot census and sample collection

During the fieldwork, 38 plots (10 m × 25 m) were set out at all major *Nepenthes* habitats on Mount Kinabalu and Mount Tambuyukon across an overall area of 700 km^2. The plot census was used to gather data on the co-occurrence of plant species in the vicinity of *Nepenthes*. Plot localities were chosen for representative ultramafic vegetation types (e.g. tall lower montane forest, short upper montane forest, sub-alpine scrub) and selected to include at least five individuals of any one *Nepenthes*-species. Further, nine plots were also established on Mount Trus Madi as a means of a non-ultramafic comparison. At each plot, the vegetation physiognomy (height and diameter of all trees >10 cm dbh) was enumerated and specimens were collected as vouchers to aid identification. All vascular plants and ferns (including epiphytes) were collected and processed as herbarium specimens and vouchers.

The ultramafic plots established on Mount Kinabalu and Mount Tambuyukon contained the following total number of *Nepenthes* individuals: *N. rajah* (584), *N. villosa* (784), *N. edwardsiana* (31) and *N. burbidgeae* (84). In each plot, soil samples and foliar samples were collected (as detailed below). Samples
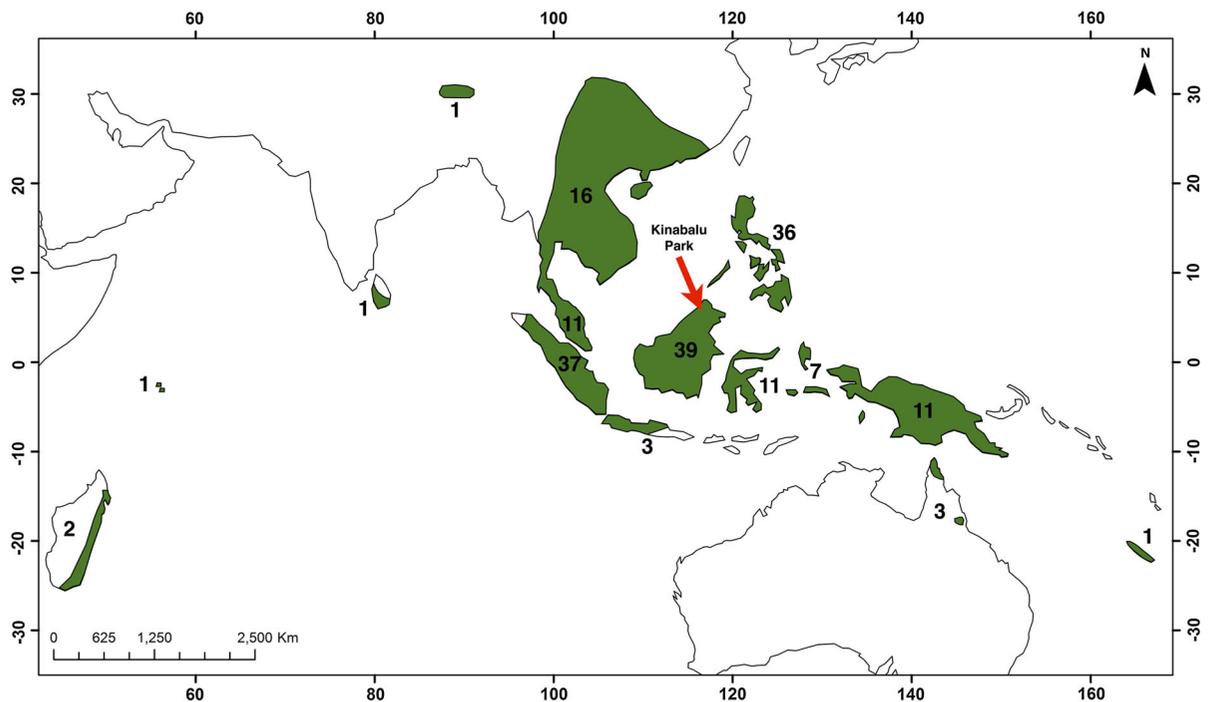
Fig. 1 Distribution of the genus *Nepenthes* (with approximate numbers of known species) and the location of Kinabalu Park in northern Borneo indicated with an *arrow*

were also collected from a number of naturally occurring hybrids: *Nepenthes rajah × fusca, Nepenthes rajah × lowii, Nepenthes rajah × tentaculata, Nepenthes × alisaputrana (N. rajah × burbidgeae), Nepenthes × kinabaluensis (N. rajah × N. villosa)* and *N. × trusmadiensis (N. macrophylla × N. lowii)*.

The plots ranged in altitude from 1332 to 2950 m asl (median 2393 m asl). The non-ultramafic plots on Mount Trus Madi contained the following total number of *Nepenthes* individuals: *N. macrophylla* (125) and *N. lowii* (36). These plots ranged in altitude from 2351 to 2642 m asl (median 2623 m asl), taking into account positional accuracy of GPS on the *z*, some plots near the summit were recorded as being up to 10 m higher than true altitude. Overall, the plot census from Kinabalu Park and Mount Trus Madi yielded a total of 47 plots containing 880 plant species in 318 genera and 119 families. Table 1 lists the studied *Nepenthes*-species of Kinabalu Park and Mount Trus Madi with general geological and altitudinal occurrence and distribution, whereas Fig. 3 shows the morphological features of these species and associated hybrids.

Soil chemistry in the root zone of *Nepenthes*

The analysis of soil chemistry is based on two sets of samples which were pooled: (a) three soil samples from each plot and (b) root zone soil samples from near individual *Nepenthes*-species. The latter were used to increase coverage of the number of *Nepenthes*-species or hybrids in areas where no full plots were made. All soil samples (1–2 kg) were collected in the mineral soil (10–25 cm deep), air-dried to constant weight and sieved to 2 mm and packed for transport to Australia. Soil pH was obtained from a 1:2.5 mixture, shaking the sample in an end-over-end shaker for 1 h, and allowing the sample to stand for 1 h before measurement. Samples (300 mg) were digested with 9 mL concentrated nitric acid (70 %) and 3 mL hydrochloric acid (37 %) in a digestion microwave, and diluted to 40 mL with triple distilled water (TDI), before analysis with Inductively Coupled Plasm-Atomic Emission Spectroscopy (ICP-AES). This 'digestion' gives 'pseudo-total' elemental concentrations. Plant-available phosphorus was extracted using the Olsen method (Olsen et al. 1954) and Mehlich-3 method (Mehlich 1984). Exchangeable cations were

Fig. 2 Map with locations of plots in Kinabalu Park with recorded *Nepenthes*-species where sample collections were made. The elevation (above sea level) is coloured, the Kinabalu Park boundary delineated and approximate outline of ultramafic outcrops provided
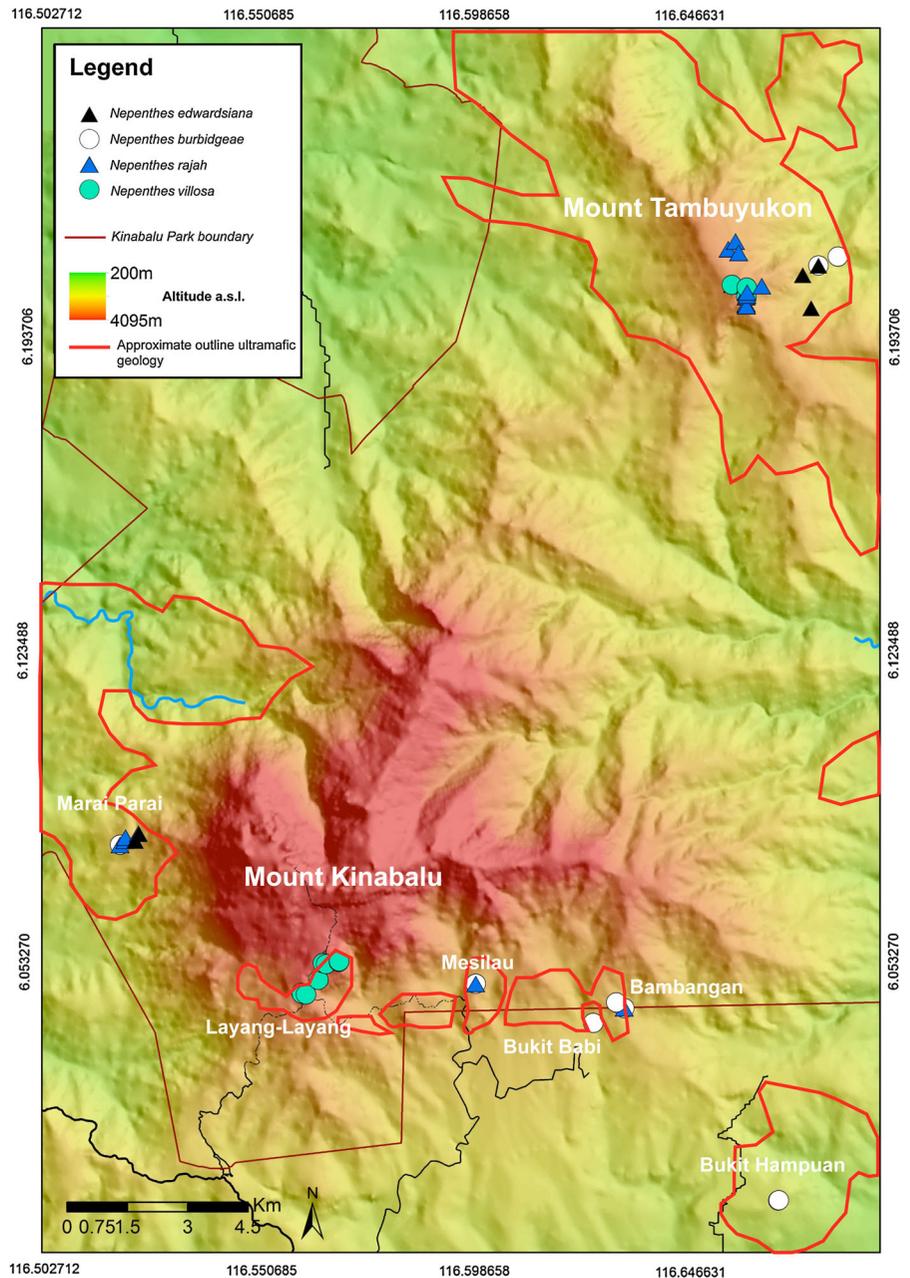
extracted with silver-thiorea (Dohrmann 2006). The 'bioavailable' fraction of trace elements was extracted with Diethylene-triamine-pentaacetic-acid (DTPA) (Lindsay and Norvell 1978 but with modifications from Becquer et al. 1995). All extractions were undertaken in 50 mL polypropylene (PP) tubes and supernatants were separated by centrifugation (4000 rpm at 10 min) before analysis with ICP-AES.

Foliar chemistry of *Nepenthes*

Full-grown leaves were collected from each *Nepenthes*, thoroughly washed with de-mineralized

Fig. 3 Visual appearance of *Nepenthes*-species and associated hybrids studied in this research

water following collection to remove dust contamination, then dried at 60 °C for 5 days in a drying oven. Foliar samples of 3–7 co-occurring dominant plant species in each plot were also collected, and treated identical to the *Nepenthes* leaf samples. All samples were weighed, crushed, and a 300-mg subsample was digested in 4 mL concentrated nitric acid (70 %) and 1 mL hydrogen peroxide (30 %) in a digestion microwave, and diluted to 40 mL with TDI water before analysis with ICP-AES. Total foliar carbon and nitrogen were analysed on a subset of leaf samples: 5 samples from each *Nepenthes*-species and 17 plant species (each) from the summit floras of Mount Tambuyukon and Mount Trus Madi. Approximately 150 mg of finely ground leaf material was weighed into tin foil boats and analysed on a LECO TruSpec CHN combustion analyser at 1100 °C.

Statistical analyses

The results from the plot soil samples (three per plot) were averaged before data analysis. Statistically significant differences between ultramafic and non-ultramafic soil chemistry were tested using Student t-tests and by Analysis of variance (ANOVA) to analyse for differences between among and between groups (i.e. individual *Nepenthes*-species). Similarly, the same tests were performed for foliar chemistry (comparing *Nepenthes* from ultramafic and non-ultramafic soils). In the multi-variate analysis using abundance data (basal area/ha for trees), there were three plots (graminoid shrub on Mount Tambuyukon with *N. rajah*) where trees (>10 cm dbh) were absent and these plots were excluded from the analysis. A minority of plots (9 out of 47) had more than one

Nepenthes-species (maximum of two co-occurring species per plot), and so for the purpose of the multivariate analysis only the *Nepenthes*-species with the greatest number of individuals in such plots were included in the analysis. Non-metric multidimensional scaling (NMDS) was used to visualise the similarities between vegetation in which *Nepenthes*-species occurred on the basis of co-occurring plant species. Finally, canonical correspondence analysis (CCA) was used to test for potential relationships between soil chemistry, *Nepenthes* and co-occurring species. All decisions about hypotheses were made against a critical value of $p = <0.01$. The statistical analyses were performed using the software packages STATISTICA Version 9.0 (StatSoft), Excel for Mac version 2011 (Microsoft), CANOCO version 5 and PRIMER Version 6 (PRIMER-E).

Results

Soil chemistry of *Nepenthes* root zone

The predominant ultramafic rock-type is peridotite, essentially a complex magnesium-iron-silicate (generalized formula: $Mg_3Si_2O_5(OH)_4$) that weathers in the humid montane conditions on Mount Kinabalu and Mount Tambuyukon to form Fe- and Mg-rich mildly acidic soils. Elemental analysis of major and trace elements (pseudo-totals) are given in Table 2. Compared to the sandstone-derived soils from Mount Trus Madi (the habitat of *N. macrophylla* and populations of *N. lowii),* the ultramafic soils have significantly lower K ($p < 0.01$), and wider-ranging concentrations of Ca and Mg, whereas Al, Na and P are similar between the ultramafic and non-ultramafic soils. The trace elements Co, Cr and Fe are significantly higher in the ultramafic soils, compared to the non-ultramafic soils from Mount Trus Madi. Table 3 shows exchangeable and extractable concentrations of elements. The cation exchange complex of the ultramafic soils is characterized by very high concentrations of exchangeable Mg (mean 7.0 cmol$^{(+)}$ kg^{-1}), whereas concentrations of exchangeable Ca, K and Na are low (comparable to Mount Trus Madi). Characteristically, the Mg:Ca quotient for all ultramafic soils is >1 (mean of 12.8), with a mean of 0.3 for Mount Trus Madi. The soils at Layang-Layang, the principal habitat of *N. villosa*, have some of the highest Mg:Ca quotients ever recorded on ultramafic soils (up to 111).

The pH in the ultramafic soils ranges from 4.4 to 7.7 (mean 6.1), and are thus significantly less acidic than the non-ultramafic soils from Mount Trus Madi (mean pH 4.1). The lesser acidity of the ultramafic soils is a result of the greater concentrations of exchangeable ions (mean CEC of 8.7 cmol$^{(+)}$ kg^{-1} vs. mean of 6.0 cmol$^{(+)}$ kg^{-1}) and thus higher buffering capacity. As a consequence of the greater soil acidity on Mount Trus Madi, exchangeable Al concentrations are also very high (mean 5.4 cmol$^{(+)}$ kg^{-1} vs. 0.2 cmol$^{(+)}$ kg^{-1}). Plant-available concentrations of Ni (as DTPA-extractable) are much higher in the ultramafic soils (mean 54.7 μg g^{-1} vs. mean of 0.1 μg g^{-1}), and such high concentrations might cause phytotoxicity. Plant-available P (as Mehlich-3 extractable) is higher (mean 9.1 μg g^{-1} vs. 3.1 μg g^{-1}) in the non-ultramafic soils of Mount Trus Madi, despite similar pseudo-total concentrations of this element in both soils; this might be explained by the very high Fe concentrations that sequester soluble P. An ANOVA shows that the differences in soil chemistry between *Nepenthes*-species are only significant ($p < 0.01$) for *N. rajah, N. villosa* and *N. macrophylla*, whereas the soils of *N. burbidgeae, N. edwardsiana* and *N. lowii* are not significantly different.

Foliar chemistry of *Nepenthes*

The 'profiles' of foliar elemental concentrations in *Nepenthes* are indicative of the nutrient-poor environments, in which these plants grow, with (very) low concentrations of Ca, K and P (Table 4). The foliar elemental concentrations of Al and S are not significantly different (i.e. $p > 0.01$) between *Nepenthes* from ultramafic and non-ultramafic soils, whereas foliar concentrations of Ca, Mg and Na are higher in *Nepenthes* from ultramafic soils, and P is lower ($p < 0.01$) compared with *Nepenthes* from non-ultramafic soils (Table 4). Concentrations of trace elements that are relatively high in ultramafic soils (Co, Cr, Fe, Mn, Ni) are low in *Nepenthes* foliage, and do not differ significantly ($p < 0.01$) from *Nepenthes* from non-ultramafic soils (*N. macrophylla* from sandstone-derived soils on Mount Trus Madi).

In order to examine possible soil-induced nutrient deficiencies, the mean foliar chemistry of *Nepenthes* was compared with the mean foliar chemistry of co-occurring plant species in the same plots (Table 5). Foliar concentrations of Al, Ca, Co, Mn and Ni are

Table 2 Soil chemistry in the root zone (including from near *Nepenthes* plants and in plots with *Nepenthes*) as 'pseudo-total' elemental concentrations ('n' denotes number of soil samples)

Species	n	Al µg g⁻¹		Ca µg g⁻¹		K µg g⁻¹		Mg µg g⁻¹		Na µg g⁻¹		P µg g⁻¹	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	3890–46,720	16,000	26–7210	2587	18–155	62	598–42,390	20,055	23–352	148	28–270	100
Nepenthes edwardsiana	7	4660–94,220	20,270	40–1650	555	3–69	3	1202–29,180	9860	26–43	15	30–82	61
Nepenthes rajah	25	1680–25,200	10,800	85–8050	1245	21–245	88	988–127,600	39,800	27–358	230	25–181	77
Nepenthes villosa	18	1630–29,500	10,500	88–1830	782	17–1056	163	2405–18,850	6966	6–150	62	41–146	103
Nepenthes × alisaputrana	2	16,900–23,320	20,110	2972–7770	5370	52–67	60	20,495–27,060	23,780	267–306	287	74–99	86
Nepenthes × kinabaluensis	1		13,000		210		291		5372		33		51
Nepenthes macrophylla (non-ultramafic)	8	1945–19,440	10,800	452–730	565	146–2200	787	71–689	316	2–124	83	42–131	83
t test ultramafic versus non-ultramafic (*p*-value)			0.6		0.2		$1.8E^{-11}$		0.03		0.2		0.8

Species	n	Co µg g⁻¹		Cr µg g⁻¹		Fe µg g⁻¹		Mn µg g⁻¹		Ni µg g⁻¹		Zn µg g⁻¹	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	17–554	176	168–8525	3030	27,650–196,600	93,360	125–6133	3000	46–2982	1172	19–185	79
Nepenthes edwardsiana	7	1–326	182	839–3400	2400	73,170–152,300	118,350	209–11,845	5360	160–2312	1065	55–162	110
Nepenthes rajah	25	34–244	143	415–3995	1665	42,975–104,700	74,040	245–6254	2570	185–3414	1122	28–102	58
Nepenthes villosa	18	5–337	106	309–2366	832	37,170–144,500	79,980	117–8370	2210	119–2742	672	22–183	65
Nepenthes × alisaputrana	2	116–229	172	3330–3500	3410	65,680–80,000	72,900	1775–3100	2440	489–624	557	71–72	72
Nepenthes × kinabaluensis	1		14		197		23,980		167		149		21
Nepenthes macrophylla (non-ultramafic)	8	0–3	2	6–32	18	113–17,490	4920	0–31	15	2–18	9	1–14	8
t test ultramafic versus non-ultramafic (*p*-value)			0.0003		0.0006		$6.4E^{-09}$		0.002		0.002		$2.3E^{-05}$

Table 3 Soil chemistry in the root zone (including from near *Nepenthes* plants and in plots with *Nepenthes*) as pH, exchangeable cations and extractable Ni and P (ranges and means)

Species	n	pH		Al cmol$^{(+)}$ kg^{-1}		Ca cmol$^{(+)}$ kg^{-1}		K cmol$^{(+)}$ kg^{-1}		Mg cmol$^{(+)}$ kg^{-1}	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	5.0–6.7	6.0	<0.01–5.8	0.4	0.1–5.4	1.3	0.02–0.3	0.1	0.7–25	7.9
Nepenthes edwardsiana	7	5.2–7.7	6.4	<0.01–5.1	0.7	0.1–1.4	0.5	0.01–0.1	0.03	0.3–8.5	2.8
Nepenthes rajah	25	5.6–7.0	6.3	<0.01–0.2	0.02	0.3–3.8	1.3	0.02–0.1	0.1	0.4–22	10
Nepenthes villosa	18	4.4–7.7	5.6	<0.01–0.7	0.2	0.1–3.9	0.9	0.02–0.2	0.1	0.1–19	3.7
Nepenthes × alisaputrana	2	6.2–6.3	6.3	<0.01	0.01	1.4–2.9	2.2	0.1–0.1	0.1	7.0–8.8	7.9
Nepenthes × kinabaluensis	1		5.6		1.56		0.18		0.03		0.2
Nepenthes macrophylla (non-ultramafic)	9	3.8–4.6	4.1	2.8–9.5	5.4	0.1–0.5	0.3	0.05–0.2	0.1	0.0–0.1	0.1
t test ultramafic versus non-ultramafic (*p*-value)			6.9E^{-11}		2.3E^{-20}		0.06		0.6		0.004

Species	n	Na cmol$^{(+)}$ kg^{-1}		CEC cmol$^{(+)}$ kg^{-1}		Mg:Ca		Ni DTPA µg g^{-1}		P Mehlich-3 µg g^{-1}	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	<0.01–0.3	0.2	0.85–36	9.8	1.1–60	15	3.2–147	64	1.8–7.2	4.0
Nepenthes edwardsiana	7	<0.10–0.1	0.1	0.50–15	4.2	1.9–73	14	4.0–125	45	1.2–2.9	2.3
Nepenthes rajah	25	<0.01–0.2	0.2	0.76–26	12	1.0–52	11	4.4–176	63	0.2–7.8	2.6
Nepenthes villosa	18	<0.01–1.7	0.3	0.24–25	5.1	0.1–111	15	0.3–166	42	1.0–4.8	2.8
Nepenthes × alisaputrana	2	0.2–0.2	0.2	8.70–12	10	2.4–6.1	4.2	35–40	37	3.7–4.1	3.9
Nepenthes × kinabaluensis	1		0.18		2.1		1.0		30		8.0
Nepenthes macrophylla (non-ultramafic)	9	<0.01–0.1	0.02	3.04–10	6.0	0.1–0.6	0.3	0.04–0.2	0.1	2.7–33	9.1
t test ultramafic versus non-ultramafic (*p*-value)			0.06		0.3		0.06		0.002		4.1E^{-06}

Mehlich-3 extractable Mehlich-extractable P, *DTPA* DTPA-extractable trace elements, *Exch.* silver-thiorea exchangeable cations, *n* denotes number of soil samples

significantly lower in *Nepenthes*, whereas concentrations of K, Na and P are higher and concentrations of Cr, Fe and Mg are not significantly different (i.e. $p > 0.01$). The higher foliar concentrations of K, Na and P, elements that can be acquired through insects/tree shrew or rat scats, indicate effective nutrient acquisition by *Nepenthes* in limiting edaphic circumstances. Elements that are primarily acquired through root-uptake such as Al and Mn are lower in *Nepenthes* compared to foliar concentrations in co-occurring plant species, as are the trace elements Co and Ni. This might be explained on account of the very small root-system of most *Nepenthes*, which probably limits uptake of soil elements.

Extractable soil macro-nutrients (Ca, Mg, K) are not significantly correlated with foliar concentrations of these elements in *Nepenthes*, except Mehlich-extractable P ($r = 0.38$, $p = < 0.001$). Separately, total foliar carbon and nitrogen were analysed on a subset of leaf samples (5 samples from each *Nepenthes*-species and 34 samples from the summit floras of Mount Tambuyukon and Mount Trus Madi). Mean foliar N in ultramafic *Nepenthes* is 9.3 mg g^{-1} (co-occurring plant species 8.6 mg g^{-1}), and for non-ultramafic *Nepenthes* 10 mg g^{-1} (co-occurring plant species 9.4 mg g^{-1}), but these differences are not significant. In the same sample set, foliar P in particular is significantly higher in non-ultramafic *Nepenthes* (0.61 and 1.16 for ultramafic and non-ultramafic *Nepenthes*, respectively, vs. mean 0.34 for co-occurring species). Figure 4 shows boxplots of foliar concentrations (K, Ca, P and S) from *Nepenthes*

Table 4 Foliar chemistry of *Nepenthes*-species and hybrids of Mount Kinabalu Park ($\mu g\ g^{-1}$) major elements (ranges and means)

Species	n	Al $\mu g\ g^{-1}$		Ca $\mu g\ g^{-1}$		K $\mu g\ g^{-1}$		Mg $\mu g\ g^{-1}$		Na $\mu g\ g^{-1}$		P $\mu g\ g^{-1}$	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	7–40	15	937–18,260	5170	1479–13,250	5700	1932–5342	3035	1217–7840	4094	234–1164	646
Nepenthes edwardsiana	8	4–57	16	1158–2795	1822	1982–18,170	9500	1526–2970	2323	427–4065	1596	485–1066	708
Nepenthes lowii (ultramafic)	4	5–15	12	668–4150	2633	1383–16,210	6625	1066–1955	1413	280–700	200	459–1711	862
Nepenthes rajah	24	2–101	17	626–7150	3215	875–24,750	7800	1449–4220	2794	280–6980	2184	259–1556	662
Nepenthes villosa	12	6–87	25	1264–5850	2178	5038–21,860	9920	1307–2985	2127	597–1869	1075	373–1188	621
Nepenthes rajah × *fusca*	1		18		7320		3360		5148		1597		402
Nepenthes rajah × *lowii*	1		14		10,380		3760		3898		541		560
Nepenthes rajah × *tentaculata*	1		15		2640		7110		513		287		237
Nepenthes × *alisaputrana*	2	15–16	16	2572–7760	5170	1880–9927	5900	1284–2218	1751	2873–3621	3247	490–524	507
Nepenthes × *kinabaluensis*	1		23		2435		13,150		2521		759		728
Nepenthes lowii (non-ultramafic)	5	7–23	13	230–1828	946	7875–11,845	9870	729–1723	1294	83–369	200	1169–1657	1486
Nepenthes macrophylla (non-ultramafic)	4	7–12	9	222–972	458	7315–20,770	12,850	1483–2628	1957	235–700	408	619–1590	920
Nepenthes × *trusmadiensis* (non-ultramafic)	2	8–25	17	211–371	291	4300–4530	4415	810–1160	985	191–279	235	695–1243	969
t test ultramafic versus non-ultramafic (*p*-value)			0.3		0.002		0.2		$1.9E^{-04}$		0.0009		$9.4E^{-07}$

Species	n	Co $\mu g\ g^{-1}$		Cr $\mu g\ g^{-1}$		Cu $\mu g\ g^{-1}$		Fe $\mu g\ g^{-1}$		Mn $\mu g\ g^{-1}$		Ni $\mu g\ g^{-1}$	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Nepenthes burbidgeae	16	0.4–1.5	1.0	1.0–16.2	4.8	3.4–6.3	4.7	14–96	31	16–277	72	1.4–28	6
Nepenthes edwardsiana	8	0.4–1.4	1.0	0.3–1.4	0.8	2.2–5.7	4.6	13–43	21	41–175	74	1.6–6.3	4
Nepenthes lowii (ultramafic)	4	1–1	1	0–3	1	2–5	3	15–92	43	67–320	177	3–6	5
Nepenthes rajah	24	0.2–1.5	0.9	0.6–67.8	9.0	2.3–7.0	4.0	11–53	19	13–597	109	2.8–42	11
Nepenthes villosa	12	0.3–2.1	1.0	0.3–5.5	1.5	1.4–6.0	3.3	15–1039	222	50–379	131	2.1–25	8
Nepenthes rajah × *fusca*	1		0.8		1.6		3.1		37		96		7
Nepenthes rajah × *lowii*	1		1.2		1.2		2.4		15		192		5
Nepenthes rajah × *tentaculata*	1		0.3		3.6		1.9		28		67		11
Nepenthes × *alisaputrana*	2	1.1–1.4	1.3	1.1–4.8	3.0	2.3–4.4	3.4	15–38	27	42–109	76	7.9–8.2	8
Nepenthes × *kinabaluensis*	1		0.5		0.5		5.2		20		181		9
Nepenthes lowii (non-ultramafic)	5	1–1	1	0.3–1	1	4–7	6	19–24	22	33–310	182	1–3	2
Nepenthes macrophylla (non-ultramafic)	4	0.1–0.5	0.4	0.2–0.6	0.4	2.1–4.5	3.4	16–17	17	25–163	88	1.5–3.8	3
Nepenthes × *trusmadiensis* (non-ultramafic)	2	0.3–0.5	0.4	0.2–0.8	0.5	3.2–4.5	3.8	14–22	18	44–76	60	2.0–4.2	3
t test ultramafic versus non-ultramafic (*p*-value)			0.014		0.2		0.2		0.4		0.5		0.02

Results are from microwave-assisted digestion with HNO_3 and H_2O_2 ('n' denotes number of soil samples)

Table 5 Comparison of foliar concentrations in *Nepenthes* and co-occurring species in the same habitat on ultramafic soils ($n = 70$ for *Nepenthes* and $n = 200$ for co-occurring species)

	Nepenthes		Co-occurring species		*p*-value
	Range µg g^{-1}	Mean µg g^{-1}	Range µg g^{-1}	Mean µg g^{-1}	
Al	1.9–101	18	14–5724	374	0.008
Ca	626–18,260	3489	2418–16,065	9047	5.56E^{-15}
Co	0.2–2.1	0.9	<0.01–5.8	1.5	0.001
Cr	0.3–68	4.8	0.8–27	3.7	0.5
Cu	1.4–7.0	4.0	1.9–5.4	3.3	0.01
Fe	11–1039	59	17–106	39	0.4
K	875–24,750	7702	1199–10,095	3913	2.16E^{-05}
Mg	513–5340	2585	1316–4275	2308	0.1
Mn	13–597	105	76–1525	575	7.34E^{-19}
Na	280–7840	2218	118–4518	1258	0.004
Ni	1–42	8	2.3–60	18	4.37E^{-07}
P	234–1711	653	207–450	303	7.04E^{-11}
S	260–964	586	579–1362	991	4.07E^{-23}

Concentrations in µg g^{-1} (ranges and means). Results are from microwave-assisted digestion with HNO_3 and H_2O_2 ('n' denotes number of foliar samples)

($n = 68$), myrtaceous shrubs (Myrtaceae, principally *Leptospermum, Tristaniopsis* and *Syzygium* $n = 98$), gymnosperms (Araucariaceae, Podocarpaceae, Phyllocladaceae, $n = 83$), graminoids (Cyperaceae, $n = 22$), Ericaceous shrubs, that are generally mycorrhizal (Ericaceae, $n = 28$), and trees and shrubs (various other families, $n = 367$) from the ultramafic soils in Kinabalu Park (unpublished data, not restricted to co-occuring species alone). Casuarinas (*Gymnostoma sumatranum*, $n = 22$) from low-altitude serpentinite soils have also been included as these have N-fixing nodules in the roots, and as such have nutrient-advantages. These data support the findings from Table 5, with significantly higher K and P in *Nepenthes* compared to other plants growing on the same soils.

Vegetation types in which *Nepenthes* occur

Ultramafic edaphic endemic *Nepenthes* of Kinabalu Park are restricted to high elevation scrublands with xeromorphic and heliophilic features such as sclerophylly, microphylly and reduced mean tree height. Such stunted forests and graminoid scrub typically occur at lower altitudes on ultramafic soils, compared to non-ultramafic soils. This spatial compression of altitudinal vegetation zonation means that the altitudinal limits for lower montane and upper montane forest types, both in term of species composition and physiognomy (structure, leaf size classes, density), are significantly shifted down (Grubb and Whitmore 1966; Proctor et al. 1988; Bruijnzeel et al. 1993; Aiba and Kitayama 1999; Ashton 2003). Figure 5 shows boxplots of tree density and altitude for plots where each *Nepenthes*-species occurred. The main vegetation types on which the ultramafic edaphic *Nepenthes* occur are (1) open upper montane forest (*N. burbidgeae, N. edwardsiana*); (2) stunted sub-alpine shrub (*N. villosa*); and (3) graminoid shrub (*N. rajah*). The specific habitats are described in more detail below (refer to the map in Fig. 2 for locality names):

Nepenthes of open upper montane forest (1200–2700 m asl)

This vegetation type is widespread on Mount Kinabalu and Mount Tambuyukon, and forms the habitat of *N. burbidgeae* and *N. edwardsiana*. The main localities include Bukit Babi, Bambangan and the slopes below the summit ridge of Mount Tambuyukon. Depending on slope aspect, the vegetation physiognomy ranges from open forest (valley, crests) morphing into sub-alpine scrub (ridges). Generally, the upper montane forest has a broken canopy 4–6 m tall and is characterized by trees in the families Myrtaceae, Podocarpaceae, Fagaceae, Lauraceae, Phyllocladaceae and Magnoliaceae. *N. burbidgeae* occurs sporadically in the most open aspects (often at the tops of steep ridges) and is never locally abundant, whereas *N. edwardsiana* is found mainly in slightly taller forest where it is generally epiphytic. The vegetation on non-ultramafic Mount Trus Madi (the habitat for *N. macrophylla* and *N. lowii*) also falls into the category of upper montane

forest and shares the same dominant families that occurs on Mount Kinabalu and Mount Tambuyukon, although the species composition differs.

Nepenthes of stunted sub-alpine scrub (2400–3100 m asl)

The stunted sub-alpine scrub is an extension of the upper montane forest that occurs below it and shares many species. It occurs mainly on exposed slopes and ridges and trees are gnarled and stunted, sometimes reduced to 'bonsais'. However, in almost all cases, the same species occur as taller trees on lower slopes. This vegetation type is the habitat for *N. villosa*. The most significant occurrences are at Layang-Layang and on the summit ridge of Mount Tambuyukon. At Layang-Layang on the south face of Mount Kinabalu (2700–3100 m asl), the vegetation is rather species-poor and dominated by *Leptospermum recurvum (*Myrtaceae*)* and *Dacrydium gibbsiae* (Podocarpaceae). *N. villosa* is extremely abundant locally (100–170 individuals per 10 m × 25 m plots).

Nepenthes of graminoid scrub (2400–3100 m asl)

Graminoid scrub occurs at two localities in Kinabalu Park: Marai Parai and the summit ridge of Mount Tambuyukon. The soils at Marai Parai are acidic and waterlogged, with a dominance of sedges such as *Costularia pilisepala* (Cyperaceae). Levels of nutrients, particularly N, are very low, indicated by the abundance of the carnivorous *Drosera ultramafica* (Droseraceae) (regionally only recorded from Marai Parai and the summit region of Mount Tambuyukon). The locally steep topography and the highly unconsolidated substrate make the area prone to landslides. The largest landslide has relatively young pioneer vegetation, which is characterized by a graminoid open structure, with small shrubs. *N. rajah* occurs throughout this area, particularly in the more open places. This is the type of locality for *N. rajah, N. edwardsiana* (in the adjoining taller forest) and *N. burbidgeae* (similarly in the surrounding forest).

The ultramafic graminoid scrub (<1 m high) on the exposed ridges above 2000-m altitude, near the summit of Mount Tambuyukon, is unique and not found anywhere else in Sabah or Borneo. *Drosera ultramafica* (Droseraceae) forms dense mats in the more open spaces. *N. rajah* is locally common and forms large rosettes (>1 m

Fig. 4 *Boxplots* of foliar elemental concentrations (K, Ca, P and S) of *Nepenthes* and ecological groups of plants (myrtaceous shrubs, gymnosperms, graminoids, ericaceous shrubs, Casuarinas, and trees and shrubs)

across) between the shrubs (with upwards of 30 individuals in many 10 m × 25 m plots).

Analysis of co-occurring plant species and vegetation physiognomy

Figure 6 presents the results of the ordination analysis (NMDS) of co-occurring plant families, genera and species per plot with individual *Nepenthes*-species as factors. In general, co-occurring plant families are not particularly well resolved, indicating that the families of plants that colonise ultramafic and non-ultramafic substrates are similar. At the genus level, patterns of resolution are somewhat clearer, with the non-ultramafic *N. lowii* and *N. macrophylla* lying between the two ultramafic groups: *N. edwardsiana—N. burbidgeae* group on one hand and the *N. rajah—N. villosa* group on the other. At the species level, the non-ultramafic *Nepenthes* are even more clearly defined, providing support for the hypothesis that many plant families and genera are common to both ultramafic and non-ultramafic substrates, but that individual species may not be.

Figure 7 shows a CCA of soil and environmental variables in relation to *Nepenthes*-species. The explanatory variables (altitude, tree density, volume and basal area and soil chemistry) in the CCA account for 72.4 % of the variation and adjusted explained variation is 56.3 % (pseudo-F = 4.5, $p = 0.002$). The results closely align with those of the NMDS (Fig. 6), but also links in soil chemistry data. The CCA shows that *N. villosa* is strongly associated with the altitudinal axis, whereas *N. burbidgeae, N. edwardsiana* and *N. rajah* are (weakly) associated with soil exchangeable Mg and pH. *N. burbidgeae* is associated with high tree volume and basal area; this exemplifies the niche for this species in montane forest. The non-ultramafic species (*N. lowii* and *N. macrophylla*) distinctly cluster towards the soil exchangeable Al, K (and bicarbonate extractable K) and Mehlich-3 and Olsen-extractable P axes. This further confirms the results of the soil analyses of the nutrient-status of the non-ultramafic and ultramafic soils associated with *Nepenthes*-species.
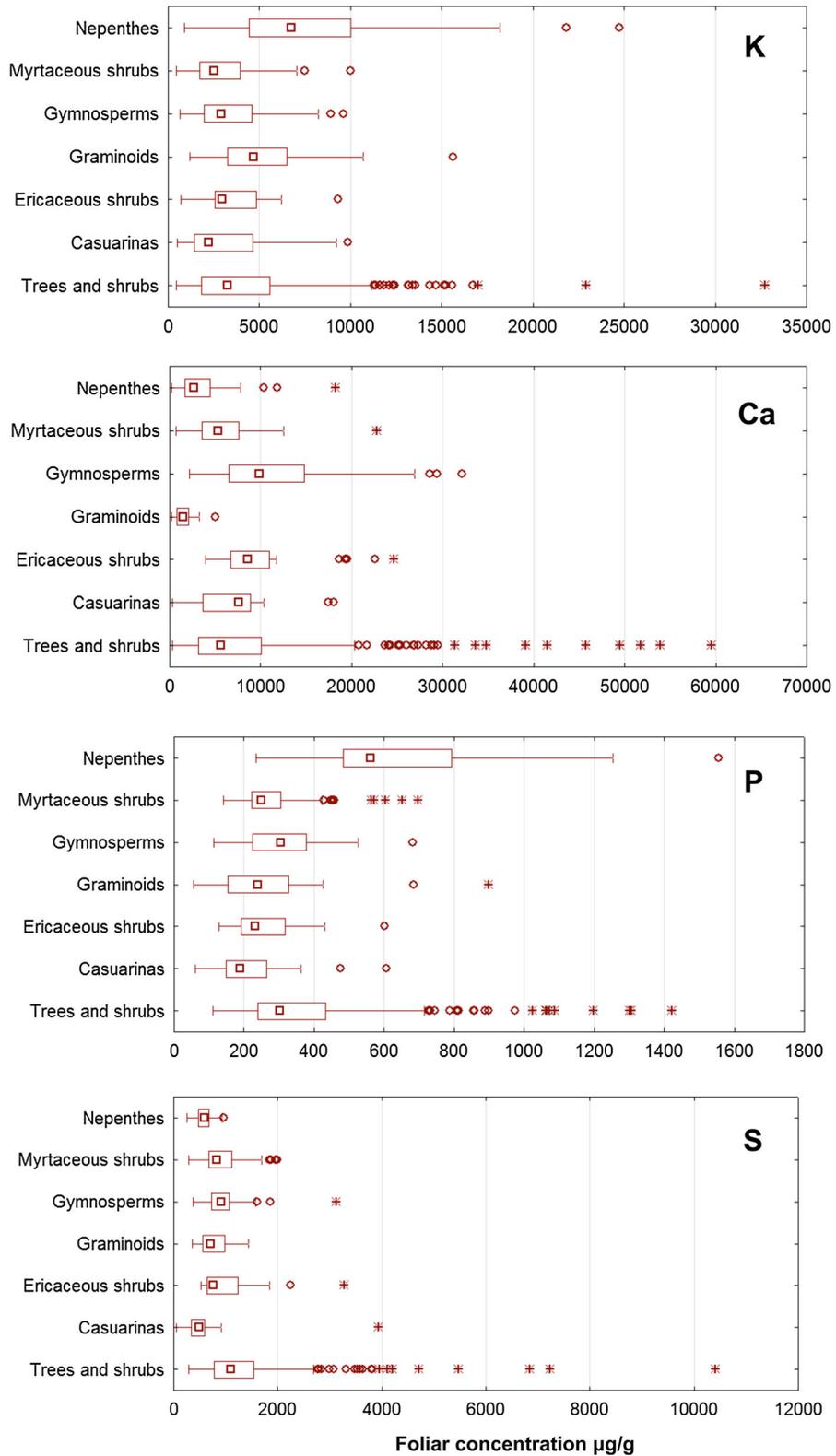
Discussion

This study aimed to elucidate habitat differentiation of ultramafic edaphic endemic *Nepenthes*-species in Kinabalu Park based on co-occurring species and soil chemistry. As such, it was hypothesized that (1) vegetation physiognomy, rather than co-occurring species, determines habitat differentiation of *Nepenthes*-species; (2) co-occurring plant species can be used to predict the occurrence of different *Nepenthes*-species; and (3) the unusual ultramafic soil chemistry is reflected in the foliar chemistry of *Nepenthes*. In light of the results obtained in this study, these hypotheses are discussed in more detail below.

Effects of vegetation physiognomy on *Nepenthes* habitat differentiation

The results (Figs. 5, 7, Supplementary Table) show that vegetation physiognomy (tree density and mean height) is the main factor influencing the distribution of *Nepenthes* and habitat differentiation for *Nepenthes*-species. *Nepenthes rajah* appears to require open habitats with very low tree densities, whereas *N. edwardsiana* prefers taller forests with higher tree densities. *Nepenthes burbidgeae* and *N. villosa* are intermediate in this respect. Whether these differences reflect demands for differing light levels or ability to compete with other plants that have different growth patterns has yet to be determined. However, it is clear that the vegetation physiognomy, under the conditions of a perhumid climate and edaphically limited soils, enables conditions suitable for *Nepenthes*; much in the same way, it enables the occurrence of a range of (endemic) ground herbs and epiphytes from the graminoid shrub on Mount Kinabalu and Mount Tambuyukon.

### Co-occurring plant species as predictors for *Nepenthes* habitats

In effect, the characteristics of the physical environment 'induces' a vegetation structure that varies among sites and produces a series of different niches that are colonised by different *Nepenthes*-species. Although the other plant species associated with these niches do not directly influence the distributions of the *Nepenthes*-species, some are characteristic of

particular niches (and, therefore, Formations). Some *Nepenthes*-species (*N. villosa, N. rajah*) are associated with more distinct assemblages than others (*N. burbidgeae, N. edwardsiana*), but there is some overlap (Fig. 6). At sites where the ranges of two or more species overlap, for example in vegetation in which *N. rajah, N. burbidgeae* and *N. edwardsiana* co-occur, they could, potentially, compete for prey. It has been suggested that co-occurring *Nepenthes*-species may avoid competition by engaging in resource partitioning (Bauer et al. 2012), and some evidence in support of this hypothesis exists (Chin et al. 2014). Although this hypothesis has yet to be tested on *Nepenthes* from Kinabalu Park, it is known that *N. rajah* exploits a nutrient source that *N. burbidgeae* and *N. edwardsiana* do not: tree shrew faeces (Chin et al. 2010). Although *N. burbidgeae* and *N. edwardsiana* grow in vegetation of similar stature (see Supplementary Table), they are rarely encountered growing in close proximity to one another, so it seems reasonable to conclude that the substantial differences in pitcher structure (see Clarke 1997) are a consequence of selective pressures other than direct competition for the same sources of supplementary N and P.

Effect of soil chemistry on *Nepenthes* foliar chemistry

The stoichiometry of foliar N, P and K in *Nepenthes* (and other plants) provides information about soil-induced nutrient limitations (Adamec 1997; Wakefield et al. 2005). Carnivorous plants are generally N + P co-limited (Ellison 2006), and carnivory has been shown experimentally to mainly supply P (Chandler and Anderson, 1976; Stewart and Nilsen 1993; Wakefield et al. 2005). This appears to be confirmed with the data from the present study, with much higher foliar P in *Nepenthes* compared to other co-occurring plant species. Recently, it was discovered that *N. rajah, N. lowii* and *N. macrophylla* have specialized nutrient acquisition strategies, other than carnivory, by having a mutualistic association with the mountain tree shrew (*Tupaia montana*) and summit rat (*Rattus baluensis*) which defecate into the pitchers (Clarke et al. 2009; Chin et al. 2010; Wells et al. 2011; Greenwood et al. 2011). In these *Nepenthes*-species, the lower lid surface presents a visual and olfactory cue (Moran et al. 2012; Wells et al., 2011) to attract tree shrews/rats who then feed on the carbohydrate-
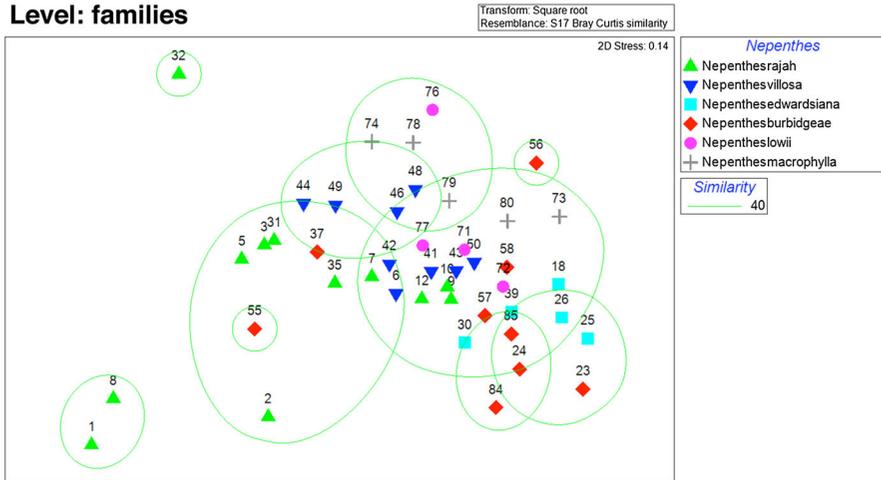
Fig. 5 *Boxplots* of tree density and altitude for each *Nepenthes*-species
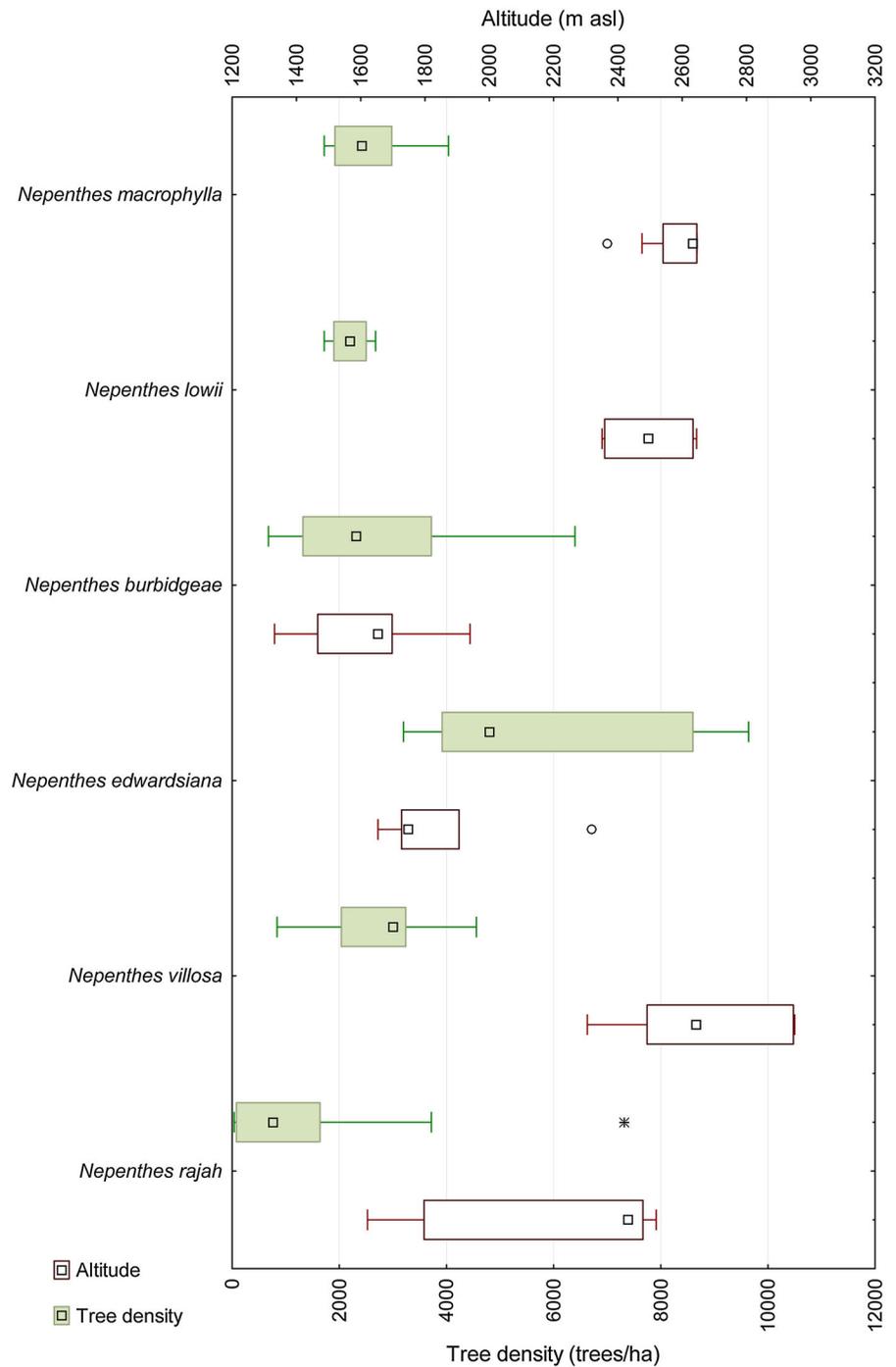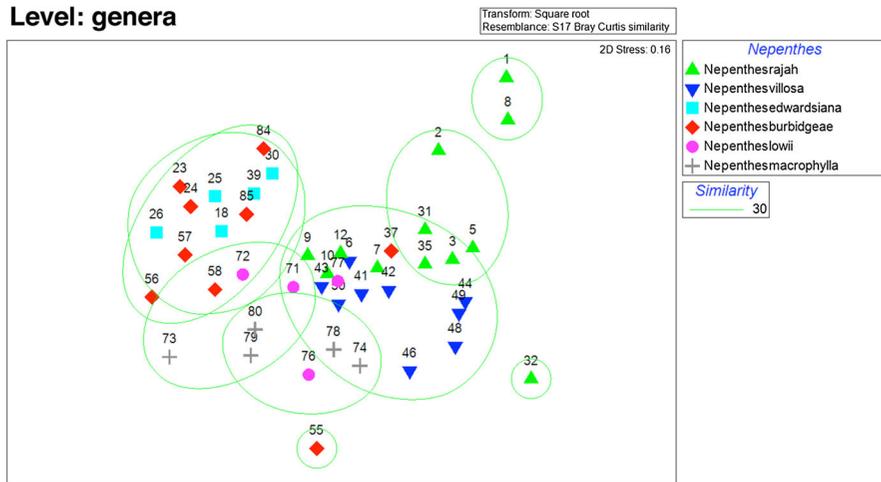
rich secretions produced by glands (Chin et al. 2010; Greenwood et al. 2011). As such, the pitchers are effectively 'lavatories' and in *N. lowii*, 57–100 % of

foliar N uptake can be supplied from tree shrew droppings (Clarke et al. 2009). Nevertheless, a comparison of *Nepenthes* and co-occurring plants in the
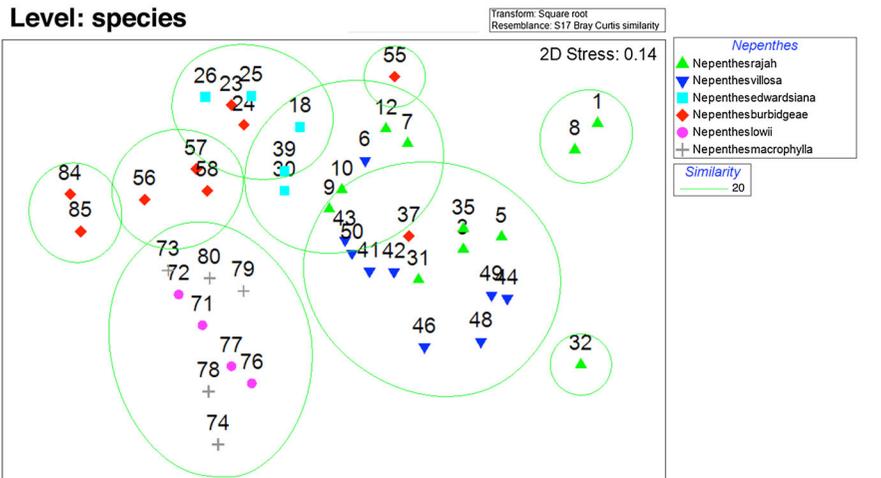
◄ **Fig. 6** Three NMDS of co-occurring plant genera in the plots with *Nepenthes* as factors, the *first* is on the level of families, the *second* on the level of genera and the *third* on the level of species. The *green circles* are the results of an analysis of similarity (using hierarchical clustering in PRIMER) between plant community associations and envelope levels of similarity either at 40 % (families), at 30 % (genera) or at 20 % (species). The *numbers* are plot identifiers

summit floras of Mount Tambuyukon and Mount Trus Madi shows that *Nepenthes* do not have higher foliar N concentrations. Uptake of elements other than N or P has only been studied in carnivorous plants that do not belong to the genus *Nepenthes* (Adlassnig et al. 2009), and their results indicate that elements likely to be supplied through insect capture or tree shrew/rat scats, such as K, may also be taken up by carnivorous plants. However, other studies, found that foliar concentrations of N, P and K were generally lower in carnivorous plants compared with non-carnivorous plants (Ellison 2006). Except pseudo-total K and Mehlich-3 P, all elements are significantly higher in ultramafic soils from Kinabalu Park, and as such, these ultramafic soils are no more nutrient deficient than non-ultramafic soils from Mount Trus Madi.

Despite radically different concentrations of siderophile elements (Fe, Ni, Co, Cr, Mn) and very high
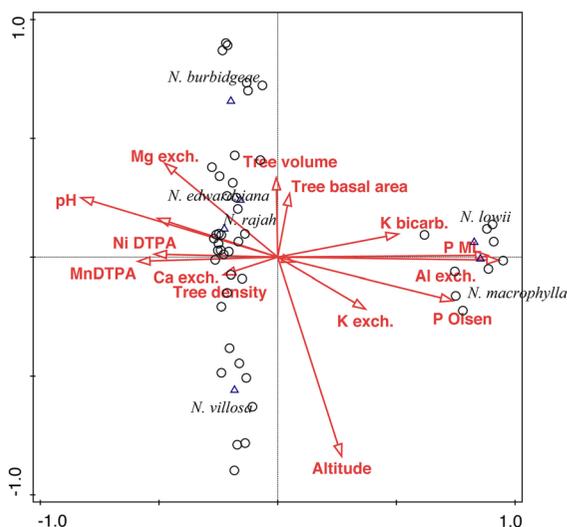
Fig. 7 CCA of soil and environmental variables in relation to *Nepenthes*-species. *ML-3* Mehlich-3 extractable P, *Olsen* NaHCO₃-extrable P, *DTPA* DTPA-extractable metals, *exch.* cations exchangeable with silver-thiorea

Mg in ultramafic soils compared to non-ultramafic soils (Mount Trus Madi), the foliar chemistry of *Nepenthes* growing in both is comparatively similar. Pseudo-total and exchangeable and extractable elements in ultramafic soils are up to orders of magnitude higher in ultramafic soils (particularly Fe, Mg, Mn and Ni) but their corresponding foliar concentrations are low. The low uptake of trace elements such as Co, Cr and Ni places *Nepenthes* into the excluder category of plants (viz. Baker 1981). This is perhaps surprising given that the lack of water-conserving physiological and morphological features (Chin et al. 2010) suggests a reasonably unconstrained opportunity for transfer of water into and through the plants, and hence the potential elemental uptake via the roots associated with that flow. It is possible that *Nepenthes* have a highly restrictive apoplastic pathway in the roots that could reduce the uptake of potentially phytotoxic elements. Such restrictive behaviour towards Ni and Mg, for example, could also limit uptake of essential elements including Ca, but additional nutrient sources could possibly mitigate such effects in the special case of *Nepenthes*.

Conclusions

The distributions of the *Nepenthes* studied here are restricted by a very unusual combination of factors, namely areas with extremely high insolation and permanently wet soils, brought about by the combined effects of an edaphic filter (ultramafic soils) and a climatic filter (altitude). Givnish et al. (1984) have effectively argued that the restriction of carnivorous plants to high insolation and permanently wet soils can be explained by considering the costs/benefits of carnivory in nutrient-poor conditions in terms of photosynthetic gains. Under such conditions, essential elements (N, P, K) are most limiting to photosynthesis and the production of biomass, and energetic investments in trap organs support a greater rate of photosynthesis per total leaf area on the scale of the plant. Given these circumstances, it seems likely that *Nepenthes* are at the 'slow-return end' of the energetic costs-benefit analysis (viz. Wright et al. 2004) with high leaf longevity, 'expensive' high-leaf mass-per-area construction, low foliar nutrient concentrations and low rates of photosynthesis and respiration (Ellison 2006, Osunkoya et al. 2007). This could also

help explain why *N. rajah*, the species restricted to the most open habitats within Kinabalu Park, has glabrous macrophyll leaves, while all other plant species in the same habitat have glaucescent microphyllous leaves. The lack of water-conserving morphologies is not a disadvantage under permanently wet conditions and, coupled with their ability to sequester limiting nutrients from the capture of animals and/or their faeces, would result in higher photosynthetic rates.

This research is the first to comprehensively focus on the auto-ecology of ultramafic edaphic endemic *Nepenthes* in Kinabalu Park and to include associated soil and foliar chemistry, but more research is needed to fully understand edaphic and climatic constraints of the *Nepenthes* habitat not only in Sabah, but also in the Philippines, where there is a paucity of research but a high richness of *Nepenthes*-species. More research is also needed in the field of population genetics to elucidate the evolution and diversification of *Nepenthes*-species within Malesia.

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