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Ecology of *Nepenthes clipeata* on Gunung Kelam, Indonesian Borneo

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ABSTRACT

Background: *Nepenthes clipeata* is a Critically Endangered plant species with the population at its only location in the wild, Gunung (Mount) Kelam in Kalimantan, Indonesia, under threat – its nutrient relationships have not been studied.

Aims: To improve understanding of the autecology of *N. clipeata* by assessing the current population and providing information on its mineral nutrient relationships.

Methods: A survey was undertaken in 2019 when population numbers and habitat preferences of *N. clipeata* were recorded. Nutrient concentrations in soil, leaves and pitcher fluid were analysed and compared with those in other *Nepenthes* species.

Results: Eighteen individuals of *N. clipeata* were found on Gunung Kelam (only one of which was female). Seven other *Nepenthes* species were found and hybrids with two of these and *N. clipeata* were observed. Although the foliar nutrient concentrations ('ionome') of *N. clipeata* appeared distinct from that of other *Nepenthes* species, with *N. clipeata* having greater nutrient concentrations, particularly nitrogen, potassium and calcium, nitrogen limitation was still prevalent.

Conclusions: *N. clipeata* still persists in the wild but with very low numbers, indicating that conservation actions are required. Along with other species of *Nepenthes*, it is limited by soil nitrogen concentrations although it has a distinct ionome derived from high foliar nutrient concentrations.

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Carnivorous plants; conservation; granite; Indonesia; ionome; stoichiometry

Introduction

Nepenthes (Nepenthaceae) is a Palaeotropical genus of dioecious pitcher plants comprising around 180 species distributed from Madagascar to New Caledonia with by far the greatest diversity in the Philippines and Indonesia. The centre of diversity of *Nepenthes* is Borneo: some species found there, such as *N. ampullaria* Jack, *N. gracilis* Korth., *N. rafflesiana* Jack and *N. reinwardtiana* Miq. (authorities follow www.ipni.org), have broad distributions, but there are also over 30 endemic species recorded from the island (Clarke 1997). Many of these are highly localised and only found on a single mountain or mountain range such as *N. faizaliana* J.H.Adam & Wilcock (Gunung Mulu), *N. murudensis* Culham ex Jebb & Cheek (Gunung Murud), *N. pilosa* Danser (Bukit Batu Lesung), *N. rajah* Hook.f. (Gunung Mulu and Gunung Tambuyukon) and, the focus of this paper, *N. clipeata* Danser. *Nepenthes* are usually found growing on infertile edaphic substrates such as heath forest white sands, ultramafic soils, mon-

tane forests and, less frequently, limestone soils. The key morphological adaptation that these species possess is their pitcher, which is a jug-like container developed at the end of the leaves that is modified to hold liquid and has a slippery peristome and/or waxy zone to trap and retain prey (Clarke 1997; Mansur 2006). However, there are a wide range of pitcher forms that have diverged evolutionarily to target contrasting prey spectra (Lam et al. 2018; Thorogood et al. 2018). These captured prey provide additional nutrients to the plant and help them to grow in nutrient-poor soils.

Nepenthes clipeata (Figure 1) is an exceptionally rare species found only on Gunung (Mount) Kelam, West Kalimantan, Indonesian Borneo. It was first discovered by Johannes Gottfried Hallier in 1894 and first determined by Danser (1928). However, this point endemic *N. clipeata* population is now severely depleted due to over-collection by illegal plant harvesting and recent fires related to El Niños (Lee 2009). In 1995, Jebb (in Simpson 1995)



Figure 1. (a) Typical habitat, (b) pitcher and (c) flowering plant of *Nepenthes clipeata* growing on the granite rock at Gunung Kelam, West Kalimantan, Indonesia. Photographic credit: M. Mansur.

reported 15 individuals remaining, Clarke (in Cheek and Jebb 2001) suggested only 2 to 6 plants might remain and Lee (2009) reported just ‘a few’ individuals remaining. Recently, Lovadi (2010) reported 260 individuals from 45 points between 765 and 875 m a.s.l. and Anonymous (2011) found an additional 63 individuals from six points between 535 and 665 m a.s.l. However, the population is still in a precarious situation in the wild with reports of illegal plant collecting as of 2019 by skilled plant ‘poachers’ and, according to the International Union for Conservation of Nature and Natural Resources (IUCN), this species is classified as ‘Critically Endangered’ (Clarke and Lee 2014).

It is considered that *Nepenthes* are nitrogen (N) limited (Brearley and Mansur 2012), but the nature of nutrient limitation may differ depending on the soil type on which plants grow. For example, whilst heath forests are considered N limited (Brearley et al. 2011; Sellan et al. in revision), ultramafic soils may be more phosphorus (P) limited (Brearley 2005; Porder and Ramachandran 2013). One way we can assess nutrient limitation is through an examination of nutrient concentrations and ratios in plant tissue (usually leaves) and, using this approach, Ellison (2006) has suggested that the majority of carnivorous plants were N and P limited but noted a lack of data for *Nepenthes*. Examination of the suite of mineral nutrients present in a plant’s tissue (‘ionome’) can shed further light on its adaptation to a given environment. For example, calcicoles (plants restricted to limestone substrates) may have a greater physiological requirement for calcium (Ca) than calcifuges that avoid this habitat (White and Broadley 2003) and plant nutrient requirements may allow hypotheses related to species edaphic preferences to be

developed. The foliar ionome in relation to substrate preference has been poorly explored for the tropical flora and not at all for *Nepenthes* species.

The aim of this study was to provide an update on the status of *N. clipeata* at Gunung Kelam and present additional data on its autecology with reference to mineral nutrition by determining the nutrient concentrations of leaves, pitcher fluid and soil around the plant. We anticipate that this new information on its nutritional requirements via examination of its foliar ionome will shed light on potential edaphic habitat preferences of this very rare species.

Materials and methods

Study site

Gunung Kelam is an immense monolithic granite dome – one of the largest in the world besides Uluru in Australia. It is located in Kelam Permai District, Sintang Regency, West Kalimantan, around 20 km from the town of Sintang and is protected as a Taman Wisata Alam (Nature Tourism Park) with an area of 520 hectares (Gustamansyah 2019). The granite dome has very steep cliffs with many areas that are inaccessible due to this topography. The climate is type ‘A’ according to Schmidt and Fergusson (Very wet) with a mean (\pm S.D.) annual precipitation of 3160 ± 661 mm between 2000 and 2017 (Mansur et al. in review).

Population estimation

A preliminary survey of the individuals of *N. clipeata* found on Gunung Kelam was made in March 2019 (two people surveying for three days), with a more extensive survey made in September 2019 (eight people surveying for three days including the use of ropes to access

steep areas) during which we conducted searches for the target species focusing on an area of about 4 ha where it was previously reported. Locations of all individuals was recorded with a Garmin GPSMAP 64s. Additional records of other species of *Nepenthes* present were made, along with their elevation and habitat type.

Nutrient relationships

Samples of leaves, pitcher fluid and soil were collected for nutrient analyses (N, P, potassium (K), Ca, magnesium (Mg) and sodium (Na)) from three plants growing at 800 to 820 m. The second youngest leaves (estimated as six months old) were collected and dried (50°C for 5 days). Soil and leaf N was analysed with a Yanako JM macro corder 1000 CN with a JMA auto sampler 1000. For other nutrients, plant and soil materials were digested in mixed acid (H₂SO₄, HClO₄ and HNO₃) for 24 hours at 170°C or filtered (pitcher fluid) and analysed for K, Ca, Mg and Na using atomic absorption spectrophotometry (Shimadzu AA-6200) and N (pitcher fluid) and P using a Shimadzu UV Mini-1240 spectrophotometer and the Nessler and vanadomolybdate colorimetric methods, respectively. Additionally, the chlorophyll concentration was measured on three leaves per plant using a Minolta SPAD-502 meter.

Statistical analyses

The nutrient composition among leaves, pitcher fluid and soil was compared using a one-way ANOVA and Tukey's test and visualised (N, P and K only) on a ternary diagram. To compare the foliar nutrient composition between *N. clipeata* and other *Nepenthes* species, another ternary diagram was created and a principal component analysis (using foliar N, P, K Ca and Mg concentrations) on scaled and centred (z-scores) values was conducted. Stoichiometric distinctiveness was calculated as in Trethowan et al. (2021) and represents the average difference between a species and all others in multivariate space, the axes of which are the concentrations of each leaf nutrient. To determine the spatial distribution of the species, Morisita's (1959) index of dispersion was calculated using a quadrat size of 50 m x 50 m with locations derived from the GPS points determined as noted above.

Results

Habitat

Nepenthes clipeata grows in open places directly exposed to sunlight on rock cliffs (Figure 1(a)) or in places with running water where the growing media is moss (*Sphagnum cuspidatum* Ehrh. ex Hoffm.; Sphagnaceae) and humus associated with rumput lambang (*Panicum sarmentosum* Roxb.; Poaceae). Some *N. clipeata* individuals were also found growing under the shade of pohon embun (*Seorsus aequatorius* Rye & Trudgen; Myrtaceae) on rock slopes associated with grasses and sedges (*Panicum sarmentosum* and *Scleria oblata* S.T. Blake ex J.Kern; Cyperaceae) and terrestrial orchids (*Arundina graminifolia* (D.Don) Hochr., *Spathoglottis gracilis* Rolfe ex Hook.f., *Paphiopedilum bullenianum* Pfitzer and *Phaius* sp., all Orchidaceae) (Mansur et al. in review). Although *N. clipeata* was found growing under the shade of trees, it was exclusively prostrate on the surface of the ground and not growing epiphytically.

Population estimate of *N. clipeata* and the presence of other *Nepenthes* species

We found 18 plants of *N. clipeata* between 765 m and 835 m a.s.l. in an area of 3.9 ha. As the majority of plants were in flower, we determined the sex of 14 of these and all but one were male. Morisita's index of dispersion was 7.71, indicating a clumped distribution. An additional seven species of *Nepenthes* were found (Table 1). *Nepenthes gracilis*, *N. mirabilis* (Lour.) Druce and *N. reinwardtiana* were generally found

Table 1. *Nepenthes* species found on Gunung Kelam, West Kalimantan, Indonesia, along with their habitat and IUCN conservation status.

Species	Habitat on Gunung Kelam	Conservation status (IUCN)
<i>N. albomarginata</i>	c. 600 m to c. 940 m in shaded areas	Least Concern (LC)
<i>N. ampullaria</i>	c. 600 m to c. 940 m in shaded areas	Least Concern (LC)
<i>N. bicalcarata</i>	540 m in shaded area	Vulnerable (VU)
<i>N. clipeata</i>	765 to 835 m in open or lightly shaded areas	Critically Endangered (CR)
<i>N. gracilis</i>	c. 300 m to c. 800 m in open areas	Least Concern (LC)
<i>N. mirabilis</i>	c. 300 m to c. 800 m in open areas	Least Concern (LC)
<i>N. rafflesiana</i>	c. 600 m to c. 940 m in shaded areas	Least Concern (LC)
<i>N. reinwardtiana</i>	c. 300 m to c. 800 m in open areas	Least Concern (LC)



Figure 2. (a) *Nepenthes clipeata* x *albomarginata* and (b) *Nepenthes clipeata* x *reinwardtiana* growing on Gunung Kelam, West Kalimantan, Indonesia. Photographic credit: M. Mansur.

growing together in open, shrubby thickets of *Gleichenia* sp. (Gleicheniaceae) and *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) between 300 and 800 m a.s.l., whereas *N. albomarginata* T.Lobb ex Lindl., *N. ampullaria* and *N. rafflesiana* were found together in more shaded areas between 700 and 900 m a.s.l. We did not enumerate the individuals of these species; we noted three individuals of *N. bicalcarata* Hook.f. at an elevation of 540 m a.s.l. in a somewhat closed area as also reported by

Hallier (1895). One of each of the hybrids between *N. clipeata* and *N. reinwardtiana* and *N. albomarginata* were found where they grew sympatrically (Figure 2).

Nutrient relationships

Nutrients were at greater concentrations in the leaves than the soil with the exception of N and Na (Table 2). The leaves were low in essential

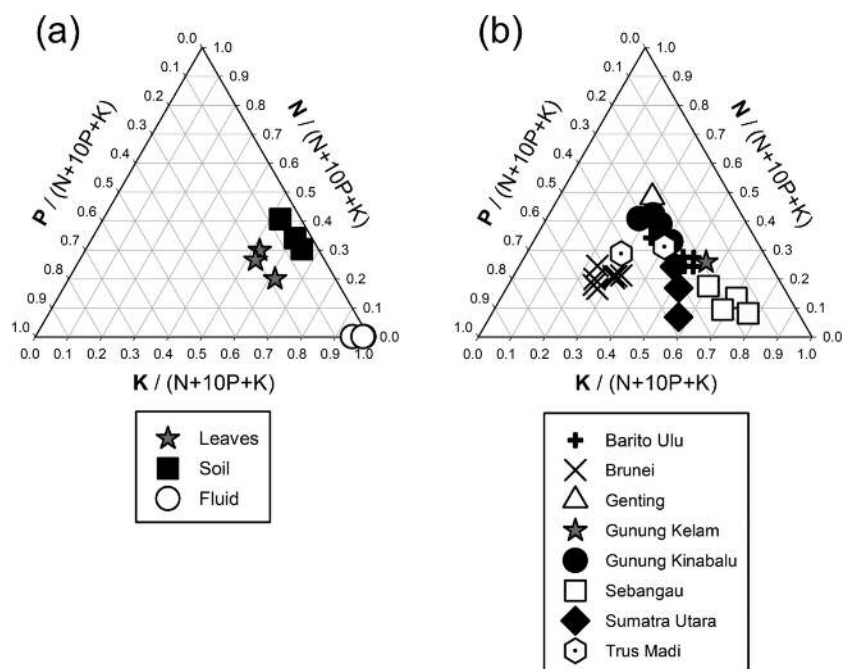


Figure 3. Ternary diagrams of (a) ratios of nitrogen, phosphorus and potassium in soil, leaves and pitcher fluid of *Nepenthes clipeata* on Gunung Kelam, West Kalimantan, Indonesia, and (b) a comparison of leaves between eight sites in Sundaland. Data are sourced from Brearley (unpubl. data) for Barito Ulu, Osunkoya et al. (2007, 2008) for Brunei, Brearley (2021) for the Genting Highlands, van der Ent et al. (2015, pers. comm.) for Gunung Kinabalu and Trus Madi, Brearley and Mansur (2012) for Sebangau and Mansur (unpubl. data) for Sumatra Utara.

Table 2. Nutrient concentrations of surrounding soil, pitcher fluid and leaves of *Nepenthes clipeata* on Gunung Kelam, Kalimantan, Indonesia ($n = 3$ for each). All values are mean \pm standard error; letters indicate significant differences for each nutrient according to Tukey's tests.

Nutrient	Soil (%)	Pitcher fluid (mg l^{-1})	Leaves (%)
N	1.02 \pm 0.14 (b)	1.98 \pm 0.58 (a)	1.58 \pm 0.28 (b)
P	0.016 \pm 0.002 (a)	8.05 \pm 4.80 (a)	0.12 \pm 0.010 (b)
K	1.71 \pm 0.02 (b)	2540 \pm 700 (a)	3.37 \pm 0.09 (c)
N:P	64.4 \pm 1.61 (c)	0.37 \pm 0.12 (a)	13.6 \pm 1.71 (b)
Ca	0.20 \pm 0.02 (a)	271 \pm 5.8 (a)	0.56 \pm 0.10 (b)
Mg	0.045 \pm 0.006 (b)	2.66 \pm 1.85 (a)	0.149 \pm 0.012 (c)
Na	0.64 \pm 0.05 (b)	909 \pm 83 (a)	0.74 \pm 0.06 (b)

nutrients with a mean N:P ratio of 13.6. The pitcher fluid was particularly low in all nutrients with the exceptions of K and Na (Table 2). The positions of all three on a ternary diagram (Figure 3(a)) were suggestive of N limitation for all of them, following the criteria of Olde Venterink et al. (2003), i.e. $N:P < 14.5$ and $N:K < 2.1$. The ternary diagram and principal component analysis examining the foliar nutrient composition of *N. clipeata* in relation to other *Nepenthes* species showed greater nutrient concentrations in *N. clipeata* than other species for many of the nutrients (Figure 3(b) and Figure 4(a)), with, notably, N, K and Ca leading to *N. clipeata* having a high stoichiometric distinctiveness (Figure 4(b)) (the majority of more distinct species were from peatland with high foliar K concentrations). The mean (\pm S.D.) chlorophyll concentration was 44.6 ± 6.6 SPAD meter units.

Discussion

We show here that the Critically Endangered pitcher plant *N. clipeata* still persists at its only known locality: Gunung Kelam in western Indonesian Borneo. However, the number of plants remains critically low and poaching of these plants still appears to be occurring (M.M. personal observation; Figure 5) despite the remaining plants being found in areas of the mountain that are difficult to access. Whilst dioecious plants are often male-biased in their populations, the significant imbalance between male and female *N. clipeata* plants at Gunung Kelam could be due to increasing levels of environmental stress known to further bias populations towards males (Munné-Bosch 2015; Hultine et al. 2016). This skewed sex ratio reduces the effective population size and has the potential to be highly limiting for the viability of the remaining population and difficult to rectify. The hybridisation seen is also suggestive of habitat disturbance following fires (see Heon and Clarke 2015). The IUCN

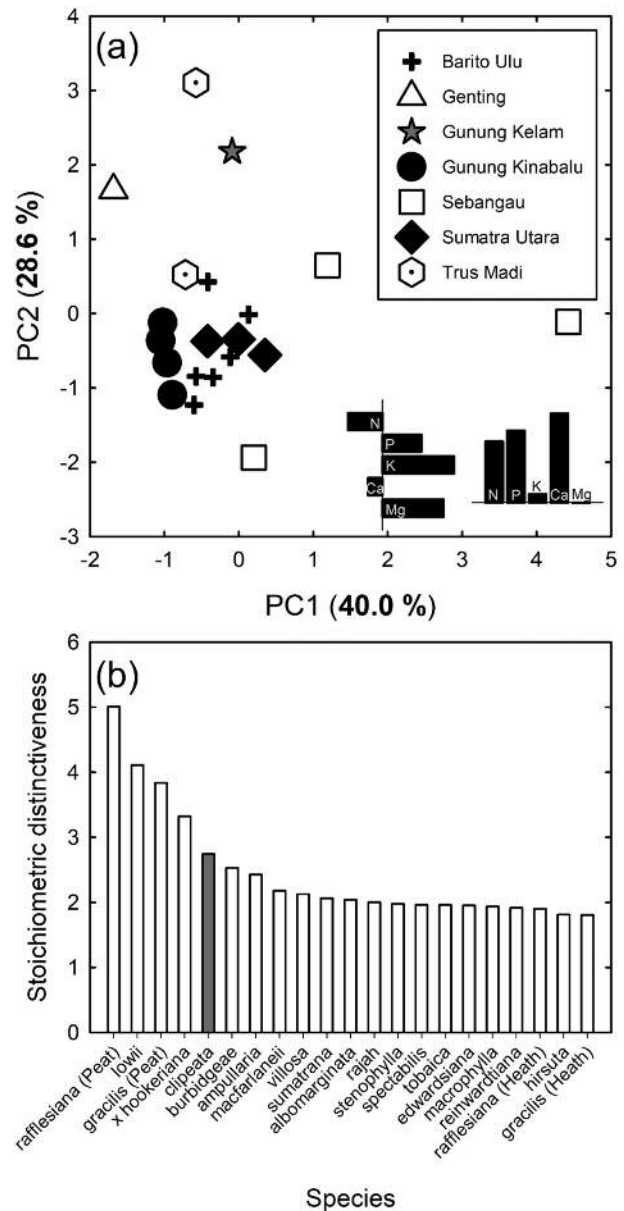


Figure 4. (a) Principal component analysis and (b) stoichiometric distinctiveness of the foliar ionome (N, P, K, Ca and Mg) of *Nepenthes clipeata* on Gunung Kelam, West Kalimantan, Indonesia, and other *Nepenthes* species from six locations in Sundaland. For (a), the two bar graphs in the bottom right of the panel represent the loadings on the two principal component axes; for (b), greater values on the y-axis indicate a more distinct ionome, i.e. the average difference between a species and all others in a multivariate space, the axes of which are the leaf nutrient concentrations. Where a habitat is noted after a species name, this indicates that this species' ionome has been determined in two contrasting habitats by different studies. See Figure 3 legend for references to data sources.

Red List classification of 'Critically Endangered A2a,d' (i.e. direct observation of a reduction in population size $\geq 80\%$ over the last 10 years due to ongoing exploitation) still appears appropriate, although it could also be considered 'Critically Endangered B2a,b(v)' (i.e. found at a single location with an area of occupancy of less than



Figure 5. Dead specimens of *Nepenthes clipeata* on Gunung Kelay, West Kalimantan, Indonesia, that are the remains of plants left by poachers. Photographic credit: M. Mansur.

10 km² showing a decline in the number of individuals). Although the population decline appears to have slowed recently, effective and repeatable measures of the population size are needed within the area of occupancy of less than 10 km² to assess recent and future changes.

The soil nutrient concentrations at the study site were fairly high as the soil was organic and mostly derived from decaying plant material. Leaf nutrient concentrations were generally greater than those in the soil as leaves are a place for storing nutrients that are absorbed from the soil. The foliar N:P ratio of c. 14 is suggestive of primary N limitation (i.e. N:P < 14.5 and N:K < 2.1 as noted above), confirming earlier results on *Nepenthes* (Brearley and Mansur 2012; Brearley 2021), and differs somewhat from other carnivorous plants that appear co-limited by N and P (Ellison 2006). When our data are compared with that of other researchers from a range of sites across Sundaland (Osunkoya et al. 2007, 2008; Brearley and Mansur 2012; van der Ent et al. 2015; Brearley 2021; Mansur, unpubl. data), it can be seen that the vast majority of *Nepenthes* species are N limited according to the criteria proposed by Ellison (2006) building on studies of Olde Venterinck et al. (2003). When compared with other sites, and similar to Sebangau peat swamp forest (Brearley and Mansur 2012), there was no indication of K deficiency as K is fairly high in granitic rocks (Manning 2010). An assessment of habitat preferences allows consideration of the breadth of habitats a plant can colonise, such as

ultramafic substrates, and we show here that *N. clipeata* appears to have an ionic composition distinct from other *Nepenthes* species, which is due to its greater nutrient concentrations not only N and K but also P and Ca, perhaps limiting it to more nutrient-rich substrates than localities at which other *Nepenthes* are found.

Interpreting N:P ratios in the pitcher fluid in terms of nutrient limitation is more challenging, but there was less N than P in the fluid indicating that it was likely to be taken up in preference and/or more rapidly. We present here one of the first chemical analyses of *Nepenthes* pitcher fluid under natural conditions, although the low N and P in the pitcher fluid were also seen by Buch et al. (2013) in young greenhouse-grown plants who also found that K and Na were high. The pitcher liquid contains a complex microbial community that is influenced by the liquid chemistry (Gilbert et al. 2020) so understanding pitcher fluid composition allows better prediction of the infaunal and microbial community.

As the plant is a creeping lithophyte, it only appears to produce one kind of pitcher, i.e. upper pitchers (Cheek and Jebb 2001). The chlorophyll concentrations were at the lower half of the range reported by Mansur (2017) for fifteen *Nepenthes* taxa and, given that chlorophyll concentrations correlate with stomatal conductance (Mansur 2017), indicate that *N. clipeata* is more water-use efficient than other *Nepenthes* species. The open environment on Gunung

Kelam, where the plants grow lithophytically, will have low humidity and the advantages of a slippery, wettable peristome are reduced if the peristome dries out rapidly after rain. The peristome of *N. clipeata* is very small and is of the 'dry type' (Bauer et al. 2012; Moran et al. 2013). Knowing this, a better understanding of its prey spectra would be informative. It would also be useful to determine if there are any unusual or species-specific infauna (e.g. Rembold et al. 2012; Karl and Bauer 2020) that are obligate mutualists of *N. clipeata* and therefore also of conservation concern.

Whilst we found 18 individuals of *N. clipeata* in total, the comparison of our population survey data with those of earlier studies is difficult as it is not known if individual plants or stems were enumerated by others. To the best of our knowledge, our study location overlaps with that of earlier researchers (Lovadi 2010; Anonymous 2011) who reported a greater number of plants than earlier reported censuses (Jebb in Simpson 1995; Clarke in Cheek and Jebb 2001; Lee 2009) as they counted each stem as an individual plant. In this study, we counted each individual stem that emerged from the ground, although it is possible that they were connected under the soil surface. In our study, *N. clipeata* was found at elevations between 765 and 835 m in open or slightly shaded areas. However, earlier reports that *N. clipeata* was found down to an elevation of 575 m suggest that it may still be possible to find individuals in other locations that are difficult to access (although the *N. clipeata* individual at an altitude of 500 m a.s.l. found by Lovadi (2010) appears to be no longer there). The population was highly aggregated, meaning that it may be at greater risk from collectors who are likely to encounter additional plants once an initial one is found. It is encouraging that local authorities are implementing efforts to prevent poaching of *N. clipeata* by blocking access to its habitat for climbers, implementing tighter security at the Park entrance (M.M. pers. obs.) and bringing legal sanctions against poachers (Pontianak Tribune 2020), but, with such a small population, the continued existence of *N. clipeata* in the wild remains tenuous.

Further conservation efforts for *N. clipeata* have been proposed for many years including propagation techniques to bring plants into cultivation, flooding the market with cultivated plants and thus relieving collecting pressure on

the remaining natural population (Lee 2009). *Nepenthes clipeata* already exists in cultivation with many plants produced by micro-propagation and, although the number of clones in cultivation is limited (Cantley et al. 2005), it represents an additional genetic source to help with *ex situ* conservation. Indeed, *ex situ* conservation through plant propagation and then re-introducing plants to their natural habitat with strict monitoring appear to be the most appropriate conservation approach in this instance. Research should also focus on understanding the environmental preferences of the species (as done partly in this paper) as well as its reproductive and regeneration dynamics and how these might differ between sexes. Further work should also examine the genetic diversity and viability of the Gunung Kelam populations and consider these in the light of the possibility for re-introduction in the future.

Conclusions

Nepenthes clipeata still persists in the wild at its only known location but with very low numbers and an imbalanced sex ratio. It appears that it has an ionic composition distinct from many other species of *Nepenthes* derived from high foliar nutrient concentrations. Illegal plant poaching still occurs, indicating that conservation actions are urgently required for the persistence of this species in its natural habitat.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Philip J. Esseen curates the UK National Collection of *Nepenthes* at Chester Zoo and is interested in actively promoting the *in situ* and *ex situ* conservation of this family and other threatened plants.

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