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ECOLOGICAL OBSERVATIONS ON NEPENTHES WEDA ON THE ISLAND OF HALMAHERA, INDONESIA

M. Mansur 1 & F. Q. Brearley 2

Nepenthes weda Cheek is a carnivorous plant species found in the Indonesian province of Maluku. It was first described in 2015, growing in metal-rich ultramafic soils in minimally disturbed forest; ecologically, this species has not been studied. The present study was conducted at Weda Bay in Halmahera, the site of a large nickel-mining complex, to determine the habitat, population, nutrient interactions and prey spectra of *Nepenthes weda*. The known distribution of *Nepenthes weda* is extended to more open lowland disturbed maquis habitats in the mining concession, increasing the extent of occupancy, although the new population was relatively small, at 46 individuals per 1000 m². Foliar nutrient concentrations were low in P and Ca due to the plant growing in ultramafic soils that are typically low in these nutrients, and foliar Ni was at concentrations similar to those for other plants at this site. The prey spectra were dominated by yellow crazy ants (*Anoplolepis gracilipes*), along with mosquito and fly larvae as inquilines. *Nepenthes weda* remains a Critically Endangered species, and we propose urgent conservation actions.

Keywords. Anoplolepis gracilipes, metals, *Nepenthes weda*, nickel, nutrient concentrations, population, serpentine, ultramafic Received 23 December 2022 Accepted 10 May 2024 Published 3 July 2024

Introduction

Indonesia is one of the world's 'megadiverse' countries formed of three major biogeographical zones: Sunda, Wallacea and Sahul. Wallacea, including the island of Halmahera, forms the transition zone between the Sunda continental shelf, containing Asian taxa, and the Sahul continental shelf, with Australasian taxa. Like many Indonesian islands, Halmahera is also geologically diverse, with a volcanic arc forming the northern peninsula, limestone forming much of the southern and eastern peninsulas, and ophiolitic ultramafic rocks forming an important portion of the eastern peninsulas. Soils derived from ultramafic rock are rich in nickel and cobalt (Proctor, 2003; Farrokhpay *et al.*, 2019), making them attractive for exploitation by mining companies. However, ultramafic soils often host species-rich and unique vegetation assemblages (Proctor, 2003; Lopez *et al.*, 2019; Garnica-Díaz *et al.*, 2023), putting biodiversity conservation and economic development though mining activities in potentially conflicting situations. Indeed, more than 95% of Indonesia's nickel is mined from Wallacea (Struebig *et al.*, 2022).

 ¹ Research Center for Ecology and Ethnobiology, Indonesian National Research and Innovation Agency (BRIN), Cibinong Science Center, Jalan Raya Jakarta-Bogor Km 46, Cibinong 16911, West Java, Indonesia.
 ² Department of Natural Science, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, England, UK. Author for corresponence. E-mail: f.q.brearley@mmu.ac.uk. Weda Bay, in eastern Halmahera, was first confirmed as having valuable nickel deposits in 1996, and mining started in 2019. In the interim period, the area was explored botanically as part of the environmental impact assessment, with a number of new species having their only known location at this highly biodiverse site described (Callmander *et al.*, 2015; Cheek, 2015; Veldkamp & Kartonegoro, 2017; Gardner *et al.*, 2021; van Welzen *et al.*, 2021).

Nepenthes is a fascinating group of carnivorous plants whose diversity is centred on the Indonesian archipelago. Nepenthes generally live in marginal soils that are poor in nutrients, but the relationship between the edaphic conditions of Nepenthes habitats and their nutrient concentrations have been little studied. The nutrients nitrogen, phosphorus and potassium often (together) limit the growth of carnivorous plants (Ellison, 2006), and so understanding these complex nutrient relationships is of value to improve knowledge of habitat requirements of Nepenthes species. In addition to macronutrients, Nepenthes plants are also able to absorb metallic micronutrients such as copper, lead and zinc, as found in N. macfarlanei Hemsl. (Brearley, 2021). While numerous papers have studied the foliar 'ionome' of plants grown in ultramafic soils (e.g. Reeves et al., 2007; Lopez et al., 2019; Trethowan et al., 2021), there is little work on Nepenthes (van der Ent et al., 2015; Brearley, provisionally accepted).

Animals trapped in the *Nepenthes* pitcher are a source of nutrients that supplement those obtained from the soil in which they grow, especially nitrogen. Several studies have shown that insects belonging to the order Hymenoptera, family Formicidae (ants), are the dominant taxa trapped in most *Nepenthes* pitchers (Kato *et al.*, 1993; Rembold *et al.*, 2010; Gilbert *et al.*, 2020; Tarigan *et al.*, 2021).

Until a few years ago, there were thought to be just three species of *Nepenthes* in Maluku. In 2015, Cheek described two new species of *Nepenthes* from Halmahera: *Nepenthes weda* Cheek (Figure 1) and *N. halmahera* Cheek. The former species was first discovered in 2012 in the Weda Bay mining concession area, growing in ultramafic soil, and its conservation status is considered to be Critically Endangered (Cheek, 2015). Cheek (2015) provides a description of the species and its characteristic features, along with those of closely related species. Given its recent discovery, limited distribution range, and potential threats to its population, it is important to provide further information on the ecology of this species. The purpose of this study was therefore to determine the population, habitat, nutrient concentrations, and prey spectra of *Nepenthes weda* at a newly discovered locality.

Materials and methods

The research was conducted in March 2022 in the area of PT Indonesia Weda Bay Industrial Park (https://iwip.co.id/) in Central Halmahera Regency, North Maluku Province, Indonesia (0°30'N, 127°55'E). The climate, according to Schmidt & Ferguson (1951), belongs to type B (wet).



Figure 1. *Nepenthes weda* at Weda Bay, Halmahera, Indonesia: A, lower pitcher; B, upper pitcher; C, male flowers; D, fruit. Scale bars (approximate): A and B, 1 cm; C, 2 cm; and D, 5 cm. Photographs: M. Mansur.

The study focused on a small area of around 0.1 ha at an elevation of 246 m a.s.l. in ultramafic maquis vegetation. A plot of 20 m \times 50 m (1000 m²) was established to determine the population of *Nepenthes weda* in its habitat. The abundance of individuals of all species present was recorded, and relative dominance and relative frequency were calculated according to Mueller-Dombois & Ellenberg (1974).

Morphological parameters of the plants were recorded, and voucher specimens were prepared and deposited at Herbarium Bogoriense (BO). Samples of leaf laminae (second leaf from the tip of the stem estimated to be 6 months old) and open pitcher fluid were taken, with three replicates each from different plants. Nutrients were analysed using the methods outlined in Mansur *et al.* (2021, 2022), but with the phenate method used for the analysis of nitrogen (Searle, 1984). Leaf chlorophyll was measured using a Konica Minolta SPAD-502 meter (Konica Minolta, Tokyo, Japan) following the protocol described in Mansur *et al.* (2022). Metallic elements were determined by atomic absorption spectrophotometry (Shimadzu AA-6200, Shimadzu, Kyoto, Japan).

Soil samples were collected from around the plants for analysis and analysed using a Rigaku NEX CG energy-dispersive X-ray fluorescence spectrometer (Rigaku, Tokyo, Japan). Semiquantitative analysis of the pitcher in-fauna was made on three mature pitchers (two lower pitchers and one upper pitcher). The pH of the pitcher fluid was measured using a Hinotek pH meter model H-009(1)A-3 (Hinotek, Ningbo, China).

Results

Nepenthes weda was found to grow in open shrubby maquis vegetation that had been disturbed by mining roads (Figure 2). The soil types at the study site (see Figure 2A) generally consisted of Cambisols and Gleysols on ultramafic substrates with sloping to slightly steep topography (10–15°). Bare soil was fairly common in the area, but *Nepenthes weda* does not appear to grow on it. The vegetation height in the habitat was typically up to 3 m for larger shrubs and included undergrowth dominated by *Dianella* sp. and *Smilax* sp., while the dominant tree species were *Ficus crassiramea* (Miq.) Miq., *Gymnostoma* sp. and *Psychotria viridiflora* Reinw. ex Blume (Table 1). The Shannon–Wiener diversity index of the plot as a whole was 1.75.

In the plot of 0.1 ha (see Figure 2A), only one species of *Nepenthes* was recorded, namely *N. weda*, with a total of 46 individuals, equating to 460 plants per hectare. Distribution among the 10 m \times 10 m subplots was random, i.e. Morisita's (1959) index of dispersion was 1.01.

The morphology of the sampled *Nepenthes weda* plants is characterised as follows. *Stem* terrestrial, climbing, terete, < 4 m long, stem diameter < 7 mm, internodes < 15 cm. *Leaves* oblong, length < 33 cm, width < 6 cm, petiole length < 6 cm, tendril length < 25 cm, mean (\pm SD) leaf thickness 0.51 (\pm 0.04) mm. *Upper pitcher* cylindrical, < 20 cm high, < 4 cm wide, peristome < 4 mm wide with ribs, single spur < 4 mm. Plants with rosette shoots (*sensu* Cheek, 2015) were also found.

| habitat of Nepenthes weda at Weda Bay, Halmahera, Indonesia | | | |
|--|--------|--------|--|
| Speciesª | RD (%) | RF (%) | |
| Nepenthes weda Cheek (Nepenthaceae) | 5.43 | 12.5 | |
| Dianella sp. (Asphodelaceae) | 31.0 | 12.5 | |
| Smilax sp. (Smilacaceae) | 31.0 | 12.5 | |
| Psychotria viridiflora Reinw. ex Blume (Rubiaceae) | 14.3 | 12.5 | |
| Ficus crassiramea (Miq.) Miq. (Moraceae) | 6.98 | 12.5 | |
| Xylopia peekelii Diels (Annonaceae) | 5.04 | 9.38 | |
| Gymnostoma sp. (Casuarinaceae) | 3.49 | 9.38 | |
| Rhodamnia blairiana F.Muell. (Myrtaceae) | 1.16 | 6.25 | |
| Macaranga tanarius (L.) Müll.Arg. (Euphorbiaceae) | 0.39 | 3.13 | |
| Planchonella vrieseana (Pierre ex Burck) Dubard (Sapotaceae) | 0.39 | 3.13 | |
| Timonius rufescens (Miq.) Boerl. (Rubiaceae) | 0.39 | 3.13 | |
| Trichospermum morotaiense Kosterm. (Malvaceae) | 0.39 | 3.13 | |

 Table 1. List of plant species and their relative dominance (RD) and relative frequency (RF) in the habitat of Nepenthes weda at Weda Bay, Halmahera, Indonesia

^a After Nepenthes weda, species are ranked according to their RD.

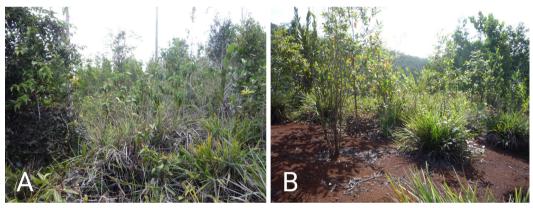


Figure 2. Habitat of *Nepenthes weda* at Weda Bay, Halmahera, Indonesia: A, in the 0.1 ha plot in which sampling was conducted in the present study; and B, about 1 km from the plot. Photographs: M. Mansur.

Soil metal concentrations were high, particularly for Cr, Ni and Mn, whose concentrations were all around 1%, but Cu could not be detected (Table 2). The most abundant macronutrients in leaves were K (0.92%) and N (0.77%) (Figure 3), with a N:P ratio of 22.0 \pm SD 0.86 and a Mg:Ca ratio greater than one. Mean leaf chlorophyll concentration was 39.9 (\pm SD 2.3) SPAD meter units. The concentrations of nutrients in the pitcher fluid were less than that in the leaves and dominated by Ca (410 \pm 33 mg/L), Mg (74 \pm 6.5 mg/L) and K (71 \pm 7.7 mg/L). Similarly, metal concentrations were lower in the pitcher fluid than in the leaves (see Table 2).

| plante at meda Bajj halmanera, maencela | | | |
|---|----------------|--------------|---------------|
| Metal | Leaves (mg/kg) | Fluid (mg/L) | Soils (%) |
| Cobalt | 87 ± 21 | 28 ± 4 | 0.21 ± 0.08 |
| Copper | 60 ± 11 | 13 ± 2 | BDL |
| Lead | 220 ± 51 | 119 ± 9 | 0.008 ± 0.002 |
| Manganese | 16 ± 5 | 4 ± 1 | 0.78 ± 0.15 |
| Nickel | 311 ± 92 | 54 ± 16 | 0.92 ± 0.22 |

Table 2. Concentration of metals in leaves and pitcher fluid of *Nepenthes weda* and soils around the plants at Weda Bay, Halmahera, Indonesia^a

BDL, below detection limits.

^a All values are mean \pm SD (n = 3 for each).

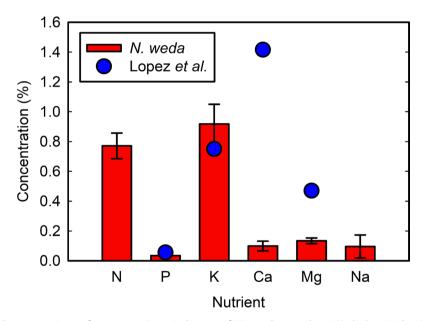


Figure 3. Concentrations of macronutrients in leaves of *Nepenthes weda* at Weda Bay, Halmahera, Indonesia. Red bars show the mean $(\pm SD, n = 3)$ concentrations for the six macronutrients. The blue dots show the mean concentrations determined by Lopez *et al.* (2019) for plants in the study area, based on results for 677 samples of non-metal-hyperaccumulating species. NB: Lopez *et al.* (2019) did not provide data for N or Na.

The pH of the pitcher fluid was $5.8 \pm SD 0.9$, and the trapped and dead insects were dominated by yellow crazy ants (*Anoplolepis gracilipes* [Smith, 1857], syn. *Anoplolepis longipes* [Jerdon, 1851]), which comprised about 97% of all insects found within the pitchers. Other animals found were mosquito larvae (c.2%) and fly larvae (c.1%), which were both observed living in the pitcher fluid as inquilines.

Discussion

When Cheek (2015) first described *Nepenthes weda*, all collections were made from lower montane forest on Bukit Limber about 7 km from the current location. In the present study, it was also found in more open shrubby maquis habitats, with its distribution extending to a lower elevation, about 250 m a.s.l. Morphologically, the plants examined broadly agree with the description of Cheek (2015).

In the study plot, the distribution of *Nepenthes weda* was random, which contrasts with the clumped distribution patterns of *N. clipeata* Danser (Mansur *et al.*, 2021). A study of *Nepenthes* species in a Sumatran montane forest (Mansur *et al.*, 2024) found *N. inermis* Danser and *N. talangensis* Nerz & Wistuba to have clumped distributions but *N. pectinata* Danser to have a more random distribution. Clearly, the scale at which the measurements are made will affect the results, but it would be interesting to determine ecological factors that lead to clumped or random distributions in this genus.

Generally, the foliar concentrations of all macronutrients were low. Lopez *et al.* (2019) described the soil and vegetation chemistry of plants from a range of locations at Weda Bay (with a focus on metal-hyperaccumulating plants), thereby generating an extensive dataset. When compared with the foliar concentrations presented in Lopez *et al.* (2019), P, Mg and particularly Ca in the leaves of *Nepenthes weda* were lower, while K was at similar concentrations. The foliar N:P ratio was the broadest so far recorded, indicating strong P limitation, which might be expected because P regularly limits plant growth in ultramafic soils (Brearley, 2005).

Foliar nutrient concentrations were lower than the mean for a number of *Nepenthes* species across their range; in particular, P and Ca were about one-third of the mean for the genus (Mansur *et al.*, 2021, 2022). Using the dataset of Mansur *et al.* (2021, 2022, 2024), combined with that of Brearley (provisionally accepted) (39 samples from 32 taxa, in total), we find significant differences between ultramafic and non-ultramafic soils in terms of *Nepenthes* foliar P (t = 4.19, p = 0.001) and K (t = 3.03, p = 0.003), but not N, Ca or Mg (p > 0.30 in all three cases). It is also notable that foliar Ca is low in *Nepenthes* generally; low Ca requirements may be advantageous on ultramafic substrates.

Foliar nickel concentrations were similar to the mean for non-hyperaccumulator plants recorded by Lopez *et al.* (2019) of 230 mg/kg, but greater than the concentration presented by Amin *et al.* (2015), who studied *Nepenthes mirabilis* (Lour.) Druce in an ultramafic wetland on Obi island, south of Halmahera, and found Ni at 37 mg/kg; foliar Co was an order of magnitude greater than that found by Lopez *et al.* (2019). There was no indication that *Nepenthes weda* could be considered a hyperaccumulator of Ni (a Ni concentration greater than 10,000 mg/kg), although foliar Co was high and around one-third of the hyperaccumulation threshold for Co of 300 mg/kg (van der Ent *et al.*, 2013). Foliar Pb concentrations were surprisingly high (< 250 mg/kg) and similar to the highest concentrations recorded by Brearley (2021) for *Nepenthes macfarlanei* in peninsular

Malaysia (< 240 mg/kg). Foliar metal concentrations in plants growing on ultramafic substrates are often greater than in those that are not, but there were no indications of metal toxicity in the case of *Nepenthes weda*.

Ants have long been known to be the dominant insect prey in *Nepenthes* pitchers (Kato *et al.*, 1993; Adam, 1997; Rembold *et al.*, 2010), often contributing more than 90% of the items found within them. However, it has been less easy to identify these ants, because they are regularly found in a state of decomposition within pitchers, although Bauer *et al.* (2011) noted that *Anoplolepis gracilipes* is a common prey species of *Nepenthes rafflesiana* Jack ex Hook. in Brunei. Halmahera is probably within the native range of *Anoplolepis gracilipes* (Lee & Yang, 2022), but it has been reported as invasive in similar ultramafic maquis in New Caledonia, which is its preferred habitat on that island (Berman *et al.*, 2013), and its presence is indicative of habitat disturbance (Latumahina *et al.*, 2015). The morphology of the pitchers of *Nepenthes weda* is of a 'dry type', with a fairly narrow peristome, which is generally considered better for trapping ants (Moran *et al.*, 2013; Clarke *et al.*, 2014). Mosquito and fly larvae have been reported as contributing to the *Nepenthes* phytotelmatic food web as inquilines in numerous other studies (Clarke, 1998).

Nepenthes weda is recorded from minimally disturbed forest (Cheek, 2015) as well as disturbed maquis vegetation at this newly noted location. Although this increases the plant's known population, area of occurrence and extent of occurrence, we do not currently suggest any changes to the proposed Red List categorisation of Critically Endangered (CR) (Cheek, 2015). The species still has a very limited distribution and small population, and so, with the expansion of industrial areas for mining, the population is under considerable threat. Nevertheless, the knowledge that the species grows in more open and disturbed habitats provides some promise for its survival, as all other collections have been made from Bukit Limber, which is the site of the richest ultramafic nickel deposits and thus under greatest threat from mining. Additional surveys of the area for *Nepenthes weda* would be valuable. Conservation actions should include moving plants to nursery areas on site where they can be reproduced by stem cuttings or seed sowing before being returned once mining operations have ceased. Seed banking of the species should also be considered to aid in the successful conservation of this rare and endangered species.

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ORCID iDs

- M. Mansur () https://orcid.org/0000-0003-0372-4699
- F. Q. Brearley (b) https://orcid.org/0000-0001-5053-5693

References

- Adam JH. 1997. Prey spectra of Bornean *Nepenthes* species (Nepenthaceae) in relation to their habitat. Pertanika Journal of Tropical Agricultural Science. 20(2–3):121–134.
- Amin R, Edraki CM, Mulligan, DR, Gultom TH. 2015. Chromium and nickel accumulation in the macrophytes of the Kawasi wetland on Obi Island, North Maluku province, Indonesia. Australian Journal of Botany. 63(7):549–553. https://doi.org/10.1071/BT15066.
- Bauer U, Grafe TU, Federle W. 2011. Evidence for alternative trapping strategies in two forms of the pitcher plant, *Nepenthes rafflesiana*. Journal of Experimental Botany. 62(10):3683–3692. https://doi.org/10.1093/jxb/err082.
- Berman M, Andersen AN, Hély C, Gaucherel C. 2013. Overview of the distribution, habitat association and impact of exotic ants on native ant communities in New Caledonia. PLoS ONE. 8(6):e67245. https://doi.org/10.1371/journal.pone.0067245.
- Brearley FQ. 2005. Nutrient limitation in a Malaysian ultramafic soil. Journal of Tropical Forest Science. 17(4):596–609. https://www.jstor.org/stable/23616596.
- Brearley FQ. 2021. Nutrient and metal concentrations in *Nepenthes macfarlanei* Hemsl. (Nepenthaceae) from a Malaysian montane forest. Notulae Scientia Biologicae. 13(2):10976. https://doi.org/10.15835/nsb13210976.
- Brearley FQ. Provisionally accepted. Foliar nutrient and metal concentrations in two *Nepenthes* species from Gunung Silam, an ultramafic mountain in northern Borneo. Plant Ecology and Evolution.
- Callmander MW, Keim AP, Buerki S, Phillipson PB. 2015. The genus *Pandanus* Parkinson (Pandanaceae) on Halmahera island (Moluccas, Indonesia) with descriptions of three new species and a key to the species on the island. Candollea. 70(2):179–195. https://doi.org/10.15553/c2015v702a2.
- Cheek M. 2015. Nepenthes (Nepenthaceae) of Halmahera, Indonesia. Blumea. 59(3):215–225. https:// doi.org/10.3767/000651915X689091.
- Clarke C. 1998. A re-examination of geographical variation in *Nepenthes* food webs. Ecography. 21(4):430–436. https://doi.org/10.1111/j.1600-0587.1998.tb00408.x.
- Clarke C, Lee CC, Enar V. 2014. Observations of the natural history and ecology of *Nepenthes campanulata*. Carnivorous Plant Newsletter. 43(1):7–13. https://dev9.carnivorousplants.org/articles/ CPNv43n1p7_13.pdf.
- Ellison AM. 2006. Nutrient limitation and stoichiometry of carnivorous plants. Plant Biology. 8(6):740–747. https://doi.org/10.1055/s-2006-923956.
- Farrokhpay S, Cathelineau M, Blancher SB, Laugier O, Filippov L. 2019. Characterization of Weda Bay nickel laterite ore from Indonesia. Journal of Geochemical Exploration. 196:270–281. https://doi.org/10.1016/j.gexplo.2018.11.002.
- Gardner EM, Arifiani D, Zerega NJC. 2021. Artocarpus bergii (Moraceae), a new species in the breadfruit clade from the Moluccas. Systematic Botany. 46(1):91–95. https://doi.org/10.1600/03636 4421X16128061189387.
- Garnica-Díaz C, Berazaín Iturralde R, Cabrera B, Calderón-Morales E, Felipe FL, García R, Gómez Hechavarría JL, Guimarães AF, Medina E, Paul ALD, Rajakaruna N, Restrepo C, Siebert SJ, van den

Berg E, van der Ent A, Velasquez G, Hulshof CM. 2023. Global plant ecology of tropical ultramafic ecosystems. Botanical Review. 89(2):115–157. https://doi.org/10.1007/s12229-022-09278-2.

- Gilbert KJ, Bittleston LS, Naive MAK, Kiszewski AE, Buenavente PAC, Lohman D J, Pierce NA. 2020. Investigation of an elevational gradient reveals strong differences between bacterial and eukaryotic communities coinhabiting *Nepenthes* phytotelmata. Microbial Ecology. 80(2):334–349. https://doi. org/10.1007/s00248-020-01503-y.
- Kato M, Hotta M, Tamin R, Itino T. 1993. Inter- and intra-specific variation in prey assemblages and inhabitant communities in *Nepenthes* pitchers in Sumatra. Tropical Zoology. 6(1):11–25. https://doi.org/10.1080/03946975.1993.10539206.
- Latumahina F, Borovanska M, Musyafa, Sumardi, Putra NS, Janda M. 2015. Ants of Ambon Island diversity survey and checklist. ZooKeys. 472:43–57. https://doi.org/10.3897/zookeys.472.8441.
- Lee CY, Yang CCS. 2022. Biology, ecology, and management of the invasive longlegged ant, *Anoplolepis gracilipes*. Annual Review of Entomology. 67:43–63. https://doi.org/10.1146/ annurev-ento-033121-102332.
- Lopez S, Benizri E, Erskine PD, Cazes Y, Morel JL, Lee G, Permana E, van der Ent E. 2019. Biogeochemistry of the flora of Weda Bay, Halmahera Island (Indonesia) focusing on nickel hyperaccumulation. Journal of Geochemical Exploration. 202:113–127. https://doi.org/10.1016/j. gexplo.2019.03.011.
- Mansur M, Brearley FQ, Esseen PJ, Rode-Margono EJ, Tarigan MRM. 2021. Ecology of *Nepenthes clipeata* on Gunung Kelam, Indonesian Borneo. Plant Ecology and Diversity. 14(3–4):195–204. https://doi.org/10.1080/17550874.2021.1984602.
- Mansur M, Salamah A, Mirmanto E, Brearley FQ. 2022. Nutrient concentrations in three *Nepenthes* species (Nepenthaceae) from North Sumatra. Reinwardtia. 21(2):55–62. https://doi.org/10.55981/reinwardtia.2022.4391.
- Mansur M, Salamah A, Mirmanto E, Brearley FQ. 2024. Ecology of *Nepenthes* on Mount Talang, West Sumatra, Indonesia. Tropical Ecology. https://doi.org/10.1007/s42965-024-00333-0.
- Moran JA, Gray LK, Clarke C, Chin L. 2013. Capture mechanism in Palaeotropical pitcher plants (Nepenthaceae) is constrained by climate. Annals of Botany. 112(7):1279–1291. https://doi.org/10.1093/aob/mct195.
- Morisita M. 1959. Measuring of the dispersion and analysis of distribution patterns. Memoirs of the Faculty of Science of Kyushu University, Series E (Biology). 2(4):215–235.
- Mueller-Dombois D, Ellenberg H. 1974. Aims and Methods of Vegetation Ecology. New York: John Wiley and Sons.
- Proctor J. 2003. Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far East. Perspectives in Plant Ecology, Evolution and Systematics. 6(1–2):105–124. https://doi. org/10.1078/1433-8319-00045.
- Reeves RD, Baker AJM, Romero R. 2007. The ultramafic flora of the Santa Elena peninsula, Costa Rica: a biogeochemical reconnaissance. Journal of Geochemical Exploration. 93(3):153–159. https://doi. org/10.1016/j.gexplo.2007.04.002.

Rembold K, Fischer E, Wetzel MA, Barthlott W. 2010. Prey composition of the pitcher plant Nepenthes

madagascariensis. Journal of Tropical Ecology. 26(4):365–372. https://doi.org/10.1017/ S026646741000012X.

- Schmidt FH, Ferguson JHA. 1951. Rainfall Types Based on Wet and Dry Period Ratios for Indonesia with Western New Guinea. Verhandelingen No. 42. Jakarta, Indonesia: Kementerian Pehubungan Djawatan Meteorologi dan Geofisik.
- Searle PL. 1984. The Berthelot or indophenol reaction and its use in the analytical chemistry of nitrogen. a review. Analyst. 109(5):549–568. https://doi.org/10.1039/AN9840900549.
- Struebig M, Aninta SG, Beger M, Bani A, Barus H, Brace S, Davies Z, De Brauwer M, Diele K, Djakiman C, Djamaluddin R, Drinkwater R, Dumbrell A, Evans D, Fusi M, Herrera-Alsina L, Iskander DT, Jompa J, Juliandi B, Lancaster LT, Limmon G, Lindawati, Lo MGY, Lupiyaningdyah P, McCannon M, Meijaard E, Mitchell SL, Mumbunan S, O'Connell D, Osborne OG, Papadopulos AST, Rahajoe JS, Rosaria, Rossiter SJ, Rugayah, Rustiami H, Salzmann U, Sheherazade, Sudiana IM, Sukara E, Tasirin JS, Tjoa A, Travis JMJ, Trethowan LA, Trianto A, Utteridge TMA, Voigt M, Winarni N, Zakaria Z, Edwards DP, Frantz L, Supriatna J. 2022. Safeguarding imperiled biodiversity and evolutionary processes in the Wallacea center of endemism. BioScience. 72(11):1118–1130. https://doi.org/10.1093/biosci/biac085.
- Tarigan MRM, Corebima AD, Zubaidah S, Rohman F. 2021. Arthropods discovered in lower and upper pitchers of *Nepenthes* at Rampa-Sitahuis Hill, North Sumatra, Indonesia. Biodiversitas. 22(12):5358– 5366. https://doi.org/10.13057/biodiv/d221217.
- Trethowan LA, Blonder B, Kintamani E, Girmansyah D, Utteridge TMA, Brearley FQ. 2021. Metal-rich soils influence tropical tree stoichiometric distinctiveness. Plant and Soil. 461(1–2):579–589. https://doi.org/10.1007/s11258-015-0468-6.
- van der Ent A, Baker AJM, Reeves RD, Pollard AJ, Schat H. 2013. Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant and Soil. 362(1–2):319–334. https://doi.org/10.1007/s11104-012-1287-3.
- van der Ent A, Sumail S, Clarke CM. 2015. Habitat differentiation of obligate ultramafic Nepenthes endemic to Mount Kinabalu and Mount Tambuyukon (Sabah, Malaysia). Plant Ecology. 216(6):789– 807. https://doi.org/10.1007/s11258-015-0468-6.
- van Welzen PC, Arias Guerrero S, Arifiani D, Bangun TJF, Bouman RW, Eurlings MCM, Gushilman I, Phillipson PB, Tabak I, Winkel E, Wurdack KJ. 2021. Weda, a new genus with two new species of Euphorbiaceae–Crotonoideae from Halmahera (North Maluku, Indonesia) and phylogenetic relationships of the Australasian tribe Ricinocarpeae. Journal of Systematics and Evolution. 59(5):1000–1017. https://doi.org/10.1111/jse.12581.
- Veldkamp JF, Kartonegoro A. 2017. New species of *Catanthera* and *Medinilla* (Melastomataceae) from Halmahera, Indonesia and a new name for a *Medinilla* from Madagascar. Reinwardtia. 16(1):25–30. https://doi.org//10.14203/reinwardtia.v16i1.3111.