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Introduction

Global research on ultramafic (serpentine) ecosystems (8th International Conference on Serpentine Ecology in Sabah, Malaysia): a summary and synthesis

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Abstract. Since 1991, researchers from approximately 45 nations have participated in eight International Conferences on Serpentine Ecology (ICSE). The Conferences are coordinated by the International Serpentine Ecology Society (ISES), a formal research society whose members study geological, pedological, biological and applied aspects of ultramafic (serpentine) ecosystems worldwide. These conferences have provided an international forum to discuss and synthesise multidisciplinary research, and have provided opportunities for scientists in distinct fields and from different regions of the world to conduct collaborative and interdisciplinary research. The 8th ICSE was hosted by Sabah Parks in Malaysia, on the island of Borneo, and attracted the largest delegation to date, 174 participants from 31 countries. This was the first time an ICSE was held in Asia, a region that hosts some of the world's most biodiverse ultramafic ecosystems. The presentations provided a cross-section of the current status of research in all aspects of ultramafic-biota relations. In this Special Issue of *Australian Journal of Botany* (Issues 1–2 combined and 3–4 combined), we have compiled a selection of papers from among the oral and poster presentations to provide insights into recent advances in geoecological and applied studies of ultramafic habitats worldwide. Here we provide a preview of select papers found in this Special Issue and summarise some of the contributions made during the 8th ICSE and describe some of the exciting challenges awaiting future research.

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Introduction

Ultramafic outcrops (also called 'serpentine') are widespread but sparse, covering roughly 3% of the Earth's surface (Guillot and Hattori 2013). The largest outcrops occur in Cuba, New Caledonia, Indonesia, the Philippines and Malaysia, whereas smaller outcrops are found worldwide, mostly along continental margins and orogenic belts (Brooks 1987; Alexander *et al*. 2007). Soils derived from ultramafic bedrock pose several edaphic challenges for plant growth, including metal toxicity, nutrient imbalances and deficiencies and, in some cases, water stress, with this last feature resulting from the often shallow, rocky, and exposed nature of the outcrops (Proctor 2003; O'Dell and Rajakaruna 2011). Ultramafic ecosystems are renowned for their high levels of plant diversity and endemism, as well as their unique plant–habitat relations (Brooks 1987; Boyd *et al*. 2004, 2009; Harrison and Rajakaruna 2011). In New Caledonia, 2150 species occur on ultramafic soils (out of a total of 3371 species for the whole flora) of which 83% are restricted to such soils (Jaffré 1992; Jaffré and L'Huillier 2010), whereas in Cuba, 920 species (approximately one-third of the taxa endemic to Cuba) are found exclusively on ultramafic soils (Borhidi 1992). Similar restrictions and notable floristic associations are also found on ultramafic outcrops of the Mediterranean region, as well as in Africa, Australia and Asia (Brooks 1987; Baker *et al*. 1992; Jaffré *et al*. 1997; Alexander *et al*. 2007; Chiarucci and Baker 2007; van der Ent *et al*. 2014*a*). The edaphic challenges associated with these island-like habitats have led to the evolution of unique ecosystems, providing model settings for exploration of biological questions at cellular and organismal levels and for the study of ecosystem-level processes (Harrison and Rajakaruna 2011).

International Conferences on Serpentine Ecology (1991–2011)

Since 1991, researchers from ~45 nations have participated in eight International Conferences on Serpentine Ecology (ICSE). Conference delegates have come from all corners of the world, including Albania, Australia, Bulgaria, Canada, China, Cuba, Czech Republic, DR Congo, France, Germany, Greece, India, Iran, Italy, Japan, South Korea, New Caledonia, New Zealand, Portugal, Russia, South Africa, Spain, Sri Lanka, UK and USA, among others. The ICSE conferences are coordinated by the International Serpentine Ecology Society (ISES), a formal research society whose members study geological, pedological, biological, and applied aspects of ultramafic ecosystems worldwide. Each conference has highlighted a region with intriguing ultramafic soil–biota relations: California in 1991 (Baker *et al*. 1992), New Caledonia in 1995 (Jaffré *et al*. 1997), South Africa in 1999 (Balkwill 2001), Cuba in 2003 (Boyd *et al*. 2004), Italy in 2006 (Chiarucci and Baker 2007), Maine and eastern Canada in 2008 (Rajakaruna and Boyd 2009) and Portugal in 2011 (with a number of articles that appeared in *Plant Ecology and Diversity*). These conferences have provided an international forum to discuss and synthesise multidisciplinary research, and have provided opportunities for scientists in distinct fields and from different regions of the world to conduct collaborative and interdisciplinary research.

The 8th International Serpentine Ecology Conference in Sabah, Malaysia (2014)

The 8th ICSE was hosted by Sabah Parks in Malaysia, on the island of Borneo. The Conference attracted the largest delegation to date, 174 participants from 31 countries (Fig. 1). The Conference took place over 3 days at the Sutera Harbour Resort in Kota Kinabalu, followed by 2 days at Kinabalu Park Headquarters. The Conference was divided into the following six sessions: (1) hyperaccumulator plants and phytotechnologies, (2) geology and soils, (3) ecology and biogeography, (4) physiology and evolution, (5) threats and conservation, and (6) diversity, systematics and taxonomy. In total, 37 poster presentations and 57 oral presentations were delivered during the conference, covering all aspects of research on ultramafic ecosystems. The mid-conference fieldtrip was to the abandoned Mamut Copper Mine (Fig. 2). At the mine, delegates had a first-hand look at the environmental damage caused by decades of mining, a harsh reality worldwide for regions with metal-rich geologies. The importance of such 'natural laboratories' for biological, ecological, evolutionary and applied research was also emphasised during the excursion. Immediately following the conference, a 1-day Pacific Rim Application and Grid Middleware Assembly (PRAGMA) special symposium was organised, entitled '*Biodiversity Computing and Data Infrastructure and Analysis*,' in which ~40 delegates participated. After the conference, many delegates took part in post-conference excursions, including climbs of Mount Kinabalu and Mount Tambuyukon, sites that are rich with rare and endemic species (van der Ent *et al*. 2014*b*, 2015; Aiba *et al*. 2015). During the excursions, delegates had the chance to witness some of the famed iconic species from Kinabalu Park, including the world's largest flower (the parasitic *Rafflesia keithii*, Rafflesiaceae), the world's largest carnivorous pitcher plant (*Nepenthes rajah*, Nepenthaceae) and spectacular orchids, such as *Paphiopedilum rothschildianum* (Orchidaceae). The conference also offered the opportunity for Sabah Parks to display and disseminate the important work it does in conservation and in advancing research on ultramafic ecosystems in Kinabalu Park and elsewhere in Sabah. This was the first time an ISCE was held in Asia, a region that hosts some of the world's most biodiverse ultramafic ecosystems (van der Ent *et al*. 2014*a*, 2015).

Current global research on the ecology and evolution of ultramafic ecosystems

The 8th International Conference on Serpentine Ecology was a forum for researchers to discuss multidisciplinary research on ultramafic ecosystems worldwide. Thus, the presentations provided a cross-section of the current status of research in all aspects of ultramafic–biota relations. In these Special Issues of *Australian Journal of Botany* (Issues 1–2 combined and 3–4 combined), we have compiled a selection of papers from among

Fig. 1. The delegates of the 8th International Conference on Serpentine Ecology in Sabah, Malaysia.

Fig. 2. Delegates at the Mamut Copper Mine during the mid-conference field trip.

the oral and poster presentations to provide insights into recent advances in geoecological and applied studies of ultramafic habitats worldwide. Below, we provide a preview of select papers found in this Special Issue, organised by the session under which those papers were presented.

Hyperaccumulator plants and phytotechnologies (Session 1)

Ultramafic soils host the greatest number of metal hyperaccumulator plants in the world, and these unique plants have been the subject of floristic, physiological, evolutionary and applied research, particularly in the past two decades (van der Ent *et al*. 2013*a*; Pollard *et al*. 2014). Hyperaccumulators have the remarkable physiological capacity to accumulate heavy metals and metalloids in leaf tissues at levels that are orders of magnitude greater than concentrations found in most other plants (Gall and Rajakaruna 2013). It is, however, a rare phenomenon, with only 1–2% of plant species found on ultramafic soils displaying this behaviour. A smaller but increasing number of plants are known as 'facultative hyperaccumulators,' hyperaccumulating heavy metals only when occurring on metal-rich soils, but also occurring commonly on normal, non-metalliferous soils (Pollard *et al*. 2014; McAlister *et al*. 2015). Currently, ~450 nickel (Ni) hyperaccumulators are known (van der Ent *et al*. 2013*a*). Hyperaccumulation is thought to have evolved to interfere with other competing plant species ('elemental allelopathy'), or to protect against insect herbivores ('elemental herbivory defence'), among other explanations (Boyd 2014). The ability of hyperaccumulators to extract substantial quantities of Ni from the soil has sparked the development of phytomining, a new technology to extract Ni by harvesting and processing of hyperaccumulator biomass (Chaney *et al*. 2007, 2014). Extensive ultramafic outcrops in Southeast Asia have the greatest potential for future phytomining operations because of the occurrence of a large number of native Ni-hyperaccumulator species (Reeves 2003; Gall and Rajakaruna 2013) and the presence of extensive lateritic Ni-mining operations in the region; these have created post-mined lands needing rehabilitation that might be useful phytomining sites (van der Ent *et al*. 2013*b*).

The session began with keynote presentations by two pioneers in the field of phytoremediation. First, Baker (2014) reviewed the development of phytotechnologies, stressing that large-scale implementation of this green technology is limited, despite some successful demonstrations in China for arsenic (As; Mandal *et al*. 2014) and cadmium–zinc (Cd–Zn) phytoextraction (Li *et al*. 2014). Second, Reeves (2014) focussed on Ni phytomining (Keeling *et al*. 2003; Boominathan *et al*. 2004; Zhang *et al*. 2014) and what is necessary to see its successful implementation. He noted areas in need of further research if phytomining is to reach its potential, including improving plant growth under metal-rich conditions, developing cultivation methods for agronomic improvement, designing management practices for dealing with pests and diseases, and creating new techniques to harvest and process biomass to maximise metal-recovery efficiency (Reeves 2014).

Manganese (Mn) hyperaccumulation was highlighted in two presentations. The first was a study on *Chengiopanax sciadophylloides* (Araliaceae) from Japan, which accumulated a maximum foliar Mn concentration of 23 000 $\mu g\ g^{-1}$ dry weight from soils containing low to normal concentrations of Mn (Mizuno *et al*. 2014). The authors obtained a highly purified Mn compound from solutions made from ashed leaves when the pH was adjusted to 8–10. Working with Australian species of the genus *Gossia* (Myrtaceae), Fernando *et al*. (2014) found that *in vivo* spatial distributions and subcellular compartmentalisation of excessively co-accumulated foliar metals, including Mn, indicated mediation by specific metal transporters at the cell boundary and/or at the tonoplast.

Study of relationships of trace element concentrations in soils and plants, and their accumulation kinetics, are crucial to design phytoextraction applications that maximise the concentration of a target element in plant biomass. Studies in New Caledonia found significant effects of leaf age on Ni and Mn accumulation, which could have implications for producing metal-rich biomass to convert into 'ecocatalysts' (Losfeld *et al*. 2014*a*). The concept of 'ecocatalysts' is based on preparation of novel catalysts from hyperaccumulator biomass. These catalysts can be used in the synthesis of molecules using what has been called 'green chemistry' (Losfeld *et al*. 2014*b*), in which these catalysts replace traditional ones. The implementation of 'ecocatalysts' in the organic chemical industry is a strong encouragement for the development of phytoextraction operations (Grison and Biton 2014). In New Caledonia, phytoextraction with *Geissois pruinosa* (Cunoniaceae), a Ni hyperaccumulator, and two subspecies of *Grevillea exul* (Proteaceae), both Mn accumulators, is underway on mine wastes (Losfeld *et al*. 2014*c*). Ongoing large-scale Ni phytomining trials in Albania were reported to yield 100 kg Ni ha^{-1}, from which a high-value product (Ni ammonium sulfate hexahydrate) was produced (Zhang *et al*. 2014). Using two native Albanian Ni hyperaccumulators (*Alyssum murale* and *A. markgrafii*, Brassicaceae), a field cropping regime was developed that yielded up to 17 t ha^{-1} biomass containing 120 kg ha^{-1} Ni (Bani *et al*. 2015). The effects of species composition (mono-cropping or co-cropping) with single and mixtures of Ni hyperaccumulator species (*Alyssum murale*, *Noccaea tymphaea*, *Leptoplax emarginata*, and *Bornmuellera tymphaea*: all Brassicaceae) were also studied in relation to the efficiency of Ni extraction; the results showed that biomass and shoot Ni concentrations (though not significant) of *B. tymphaea* increased in the co-cropping system (Rue *et al*. 2015).

Recent discoveries of Ni-hyperaccumulator plants were reported from the Philippines, in the islands of Palawan, Surigao and Zambales, where three species of *Phyllanthus* (Euphorbiaceae) were found containing >1% foliar Ni. They include *Phyllanthus balgooyi* with 7638 μg g^{-1} Ni and *P. erythrotrichus* and *P. securinegoides*, both with >10 000 μg g^{-1} Ni (Quimado *et al*. 2015). Five new Ni hyperaccumulators were also reported from Sri Lanka (*Euphorbia heterophylla* (Euphorbiaceae), *Vernonia cinerea* (Asteraceae), *Flacourtia indica* (Salicaceae), *Olax imbricata* (Olacaceae) and *Toddalia asiatica* (Rutaceae); Iqbal and Rajakaruna 2014), adding to the three previously documented for the island by Rajakaruna and Bohm (2002). The occurrence of copper (Cu) hyperaccumulation among some ultramafic plants, a phenomenon previously reported only for five species from Sri Lanka (Rajakaruna and Baker 2004), was also recently confirmed for Malaysia and Brazil (van der Ent and Reeves 2015). Interestingly, a laboratory study by Ghasemi *et al*. (2015*a*) showed that, in the presence of Ni, Cu is accumulated in both roots and shoots of Ni-hyperaccumulating *Alyssum* spp. but not in their non-ultramafic congeners. Ghasemi *et al*. (2015*a*) suggested that Cu hyperaccumulation in the presence of Ni, an abundant metal found in serpentine soils, may be common. In Indonesia, foliar elemental concentrations were studied in *Emilia sonchifolia* (Asteraceae) grown in top and overburden soils of the local Ni mines (Tjoa and Barus 2014). Their work showed that, although this species produced two- to five-fold greater shoot biomass when grown in top soils, Ni-removal rate was higher in overburden soils (which had a higher Ni concentration). The chromium (Cr) phytoextraction potential of *Brassica juncea* (Brassicaceae) was studied in Sri Lanka, showing that accumulation was dependent on the genotype and the ionic concentration of the medium; highest foliar accumulation (3511 μg g^{-1}) occurred when plants were supplied with 200 μg mL^{-1} of Cr(VI) (Wijethunga *et al*. 2014).

The use of plants for rehabilitation of mineral wastes was demonstrated with *Typha angustifolia* (Typhaceae) at the former Mamut Copper Mine (Saibeh *et al*. 2014) and by a study on relationships among soil microbial properties, plant cover and biomass on ultramafic tailings in South Africa (Smith *et al*. 2014). In the latter case, marked differences in soil microbial biomass and community structure were observed between the rock dump and the tailings dam, with the highest plant biomass being recorded at waste piles of intermediate ages and on the moist, eastern aspects of the piles. The importance of studying microbial relations in phytoremediation efforts was also emphasised in a study examining the potential of *Hieracium pilosella* (Asteraceae) for phytoremediation in the presence of soil microbes (Ogar *et al*. 2014). This study showed beneficial effects of microbes on plant growth; dry mass of shoots and roots increased significantly when plants were inoculated with mycorrhizal fungi and nitrogen-fixing bacteria. Seneviratne *et al*. (2015) also showed that the inoculation of ultramafic soils with bacteria and fungi can enhance soil quality and promote plant growth in the presence of heavy metals. Inoculation with mycorrhizal fungi and addition of P can have plant species-specific growth effects, as shown by a study investigating whether P addition can stimulate plant growth without inhibiting mycorrhizal formation (Amir and Gensous 2014).

Geology and soils (Session 2)

Ultramafic rocks containing the serpentine group of minerals, including antigorite, chrysotile and lizardite, have their origins within the Earth's upper mantle. These rocks often form large massifs and belts or tabular bodies along continental margins, faults and shear zones. Common ultramafic rock types include peridotites (including dunite, wehrlite, harzburgite, lherzolite) and the secondary alteration products (serpentinites) formed by their hydration within the Earth's crust, via a process known as serpentinisation (Evans *et al*. 2013). Serpentinisation creates strongly reducing conditions, including fluids enriched with hydrogen and methane; compounds which chemosynthetic microbes can exploit for metabolic energy (Cardace and Hoehler 2011; McCollom and Seewald 2013; Cardace *et al*. 2014). Detailed accounts of the origins of serpentinites, including their mineralogy, petrology, weathering and geographic distribution, can be found in Coleman and Jove (1992), Moores (2011) and Hirth and Guillot (2013). Over 60% of the global Ni supply comes from Ni laterite ores produced from the intensive weathering of serpentinites found under humid, tropical conditions (Butt and Cluzel 2013). Ultramafic soils are weathered products of serpentinite and other ultramafic rocks. Ultramafic bedrock type, drainage conditions and weathering intensity all contribute to differences in pedogenesis and availability of elements, including Ni (Echevarria 2014). For example, ultramafic soils formed by the weathering of peridotite or serpentinite (ultramafic rocks that are chemically similar, yet mineralogically distinct) show appreciable differences in geomorphic and pedologic features (Alexander and DuShey 2011). For a summary of the developmental processes of ultramafic soils see Brooks (1987) and Alexander *et al.* (2007). Ultramafic soils are generally deficient in plant essential nutrients such as nitrogen (N), phosphorus (P), potassium (K) and sulfur (S), have a calcium : magnesium (Ca : Mg) ratio <1, and have elevated concentrations of heavy metals such as Ni, cobalt (Co), Cd and Cr. Although physical features of ultramafic soils can vary considerably from site to site (and within a site), ultramafic soils are often found in open, steep landscapes with substrates that are generally shallow and rocky, and that often have reduced capacity for moisture retention. Extensive mining in regions overlying ultramafic bedrock has led to degraded landscapes needing restoration. Careful management of the topsoil (extracted before the mining disturbance) can maximise biodiversity on newly restored soils because the topsoil can reintroduce both native seeds and microbes to a site under restoration (Bordez *et al.* 2014). A study by Mori (2014) examined the potential for greenhouse gas emissions (CO_2, CH_4, N_2O) from undisturbed forest soils on different parent materials (sedimentary rock and serpentine rock) along an altitudinal gradient (700, 1700, 2700 and 3100 m asl) on Mount Kinabalu, Borneo. His work suggested that carbon fluxes decrease with increasing altitude, implying that lower temperature inhibits microbial activities. N_2O emissions, however, were not altitude-dependent, but were lower on ultramafic soils than on sedimentary soils, likely because of the lower N availability and closed N cycle in ultramafic soils, including lower inorganic N, nitrification potential, microbial N, and higher $NH_4^+ : NO_3^-$ ratio. Whether ultramafic rocks can save the world from increased carbon emissions has also been a focus of study (Power *et al.* 2013). Mg-rich serpentinite and related rocks can react with water and CO_2 to form magnesium carbonate plus silica, thus sequestering potentially damaging CO_2 emissions (Maroto-Valer *et al.* 2005; Yang *et al.* 2008). This technique, if implemented, might have a drastic impact on the unique biota of ultramafic areas.

Ecology and biogeography (Session 3)

The unique features of ultramafic habitats can have important effects on organismal interactions, providing many stimulating avenues for research. Ultramafic sites may contain unique species of bacteria, fungi, plants and animals, and these often are assembled into communities distinct from surrounding areas. Floras of ultramafic sites have attracted considerable attention at past International Conferences on Serpentine Ecology, and the 2014 Conference was no exception. In this session, comparison of ultramafic and non-ultramafic forests on Mount Kinabalu (Aiba *et al.* 2015), description of the ultramafic flora of Sri Lanka (Iqbal and Rajakaruna 2014) and a review (Siebert 2014) of South African ultramafic-ecology research (which showed that much work there has focussed on species descriptions and investigation of diversity patterns) added to our global knowledge of ultramafic plant ecology. Several contributions also added to our floristic knowledge for ultramafic sites in Malaysia (Damit *et al.* 2014; Majapun *et al.* 2014; Pereira *et al.* 2014; Sabran *et al.* 2014), including studies conducted at the venue for the poster session, Kinabalu Park (Karim and van der Ent 2014; Sumail and van der Ent 2014). Other presentations contributed floristic information from South Africa (Frisby *et al.* 2014), Japan (Mizuno and Kirihata 2015) and Iran (Mohtadi *et al.* 2014). Burgess *et al.* (2015*a*) documented successional changes that have occurred on ultramafic grasslands in the Mid-Atlantic region of the USA, showing that grass-dominated sites have shifted to forests over a decades-long time frame.

Rajakaruna and Boyd (2014) pointed out that ultramafic faunas are little studied compared with ultramafic floras. Contributions from past International Conferences on Serpentine Ecology (Chazeau 1997; Jourdan 1997; Cañamero *et al.* 2004) have added to our knowledge of fauna. This tradition continued at the 2014 Conference with presentations by Chung *et al.* (2014) on insects from ultramafic sites in a Malaysian forest reserve and Homathevi *et al.* (2014) on termite diversity on ultramafic sites on Mount Tambuyukon, Sabah. Lichens of serpentine areas are receiving more study, in part because of work stimulated by presentations at past conferences (e.g. Paukov 2009). The 2014 Conference received new contributions on the lichen floras of ultramafic areas in Europe (Paukov *et al.* 2014; Favero-Longo *et al.* 2015) and the north-eastern US (Medeiros *et al.* 2014). In contrast to plants and lichens, bacteria and mycorrhizal communities seem less affected by ultramafic soils. For example, Oline (2006) found little evidence that there is a unique ultramafic-soil bacterial flora. Venter *et al.* (2015) examined soil algae and cyanoprokaryotes in ultramafic and non-ultramafic soils in South Africa and reached a similar conclusion, but did discover that some species were unique to the ultramafic communities. In a review produced from the 2011 conference, Southworth *et al.* (2014) found little evidence that mycorrhizal fungal communities are edaphically specialised. This may stem from ectomycorrhizal fungi being less inhibited by edaphic stressors than are plants growing in ultramafic soils (Branco and Ree 2010).

One fascinating component of many ultramafic floras are metal-hyperaccumulator plants. Researchers at the 2014 conference continued to catalogue these species, describe their associates, and explore their physiology and ecology. van der Ent *et al.* (2015) added 19 new Ni-hyperaccumulator species to the five previously recorded from ultramafic soils in Sabah (Malaysia), illustrating the potential for new discoveries of these unusual plants. Mesjasz-Przybylowicz and Przybylowicz (2014) highlighted intensive and wide-ranging research accomplished in South Africa on several Ni-hyperaccumulator plant species, including investigations of the mycorrhizal and herbivore associates of these plants (also see Mesjasz-Przybyłowicz and Przybyłowicz 2011). Metal-hyperaccumulator plants may use metals for defence or the metals may have other functions (such as elemental allelopathy or drought resistance), as recently reviewed by Boyd (2014). In a contribution from the 2006 conference, Boyd (2007) pointed out that most studies of metal hyperaccumulation as a plant defence have focussed on whether metals increase plant resistance to herbivore attack. But tolerance of herbivory (ability to withstand damage) may be another plant defence tactic affected by metal hyperaccumulation. Palomino *et al*. (2007) first addressed this question in a paper published in the 2006 conference proceedings, finding significantly increased tolerance by *Noccaea fendleri* subsp. *glauca* to herbivore damage when plants hyperaccumulated Zn. Mincey and Boyd (2014) showed elevated tolerance of herbivory by a Ni-hyperaccumulator species (*Streptanthus polygaloides*, Brassicaceae), confirming and extending the earlier work with Zn.

Finally, the patchiness of ultramafic habitats at many sites can have important impacts on ecological relationships (e.g. pollination, seed dispersal) that can affect gene flow and speciation. For example, research presented at the 2011 conference (Spasojevic *et al*. 2014) explored patterns of seed-dispersal syndromes in Californian ultramafic and non-ultramafic floras, including the influence of ultramafic patch size. Substrate type significantly influenced seed dispersal by vertebrates and wind, but patch size did not have an important effect. At the 2014 Conference, the patchiness of ultramafic habitats was evident by presentations from many locations, including, for example, South Africa, Malaysia and the Philippines. In this session, Porembski (2014) pointed out similar patchiness of other geological substrates, such as granitoid and ironstone outcrops, that also results in unique communities. More recently, other edaphic island communities, such as those found on gabbro (Medeiros *et al*. 2015) and gypsum (Moore *et al*. 2014; Escudero *et al*. 2015), have also received close attention as settings comparable to ultramafic habitats for examining ecological and evolutionary theory (Harrison and Rajakaruna 2011). Some of the floristic works discussed above have important biogeographic aspects, because they document the distributions of species across these patchy edaphic landscapes. Other contributions to this session targeted specific biogeographic relationships. One such biogeographic concept, Rapoport's rule (Veter *et al*. 2013), was the topic of the presentation by Whitman and Russo (2014). Rapoport's rule states that the size of a species' range increases as altitude or latitude increases, and Whitman and Russo (2014) found that the rule applied to soil-generalist species on Mount Kinabalu, but not to ultramafic-soil specialists. They suggested that edaphic specialisation limits a species range of climatic tolerance (also see Fernandez-Going 2014). A study by Ghasemi *et al*. (2015*b*) examined environmental-stress sensitivity under different Ca : Mg ratios by a ultramafic endemic and its non-ultramafic congener. Their study suggested that, under higher Ca : Mg ratios (characteristic of non-ultramafic soil), the ultramafic endemic has reduced tolerance to higher N and increased temperature. The implication of this study is that ultramafic endemics may be more susceptible to human-driven climate change-associated stressors, such as atmospheric N deposition (Pasari *et al*. 2014), than non-ultramafic species. The presentation by Burge (2014) also addressed the impact of ultramafic soils on plant climatic niches. Focusing on soil generalists from California USA, this study examined whether ultramafic soils allow plants to move outside their climatic niches. This was indeed the case for both upper and lower limits of species distributions. It was suggested that at low elevations, ultramafic soils provide a refuge from competition, whereas at high elevations, the effect of cold is magnified by infertile ultramafic soils (Burge and Salk 2014).

Physiology and evolution (Session 4)

Because of the high degree of abiotic stress on ultramafic sites, ultramafic-associated biota are model organisms for the study of adaptation (O'Dell and Rajakaruna 2011). The low Ca : Mg ratio of ultramafic soils is a major challenge to plant growth and mechanisms to deal with this nutrient imbalance are key to ultramafic tolerance. These mechanisms include tolerance of high concentrations of soil Mg, reduced absorption of Mg, or higher absorption of Ca (Palm and Van Volkenburgh 2014). In addition, low macronutrient concentrations, high concentrations of some heavy metals, and low water availability are also important factors that must be tolerated by ultramafic plants. Several poster and oral presentations at the conference addressed ultramafic tolerance with respect to heavy metals and other nutrient imbalances in plants (Doronila *et al*. 2014; Echevarria *et al*. 2014; Pollard and Smith 2014; Teptina and Paukov 2014; Ghaderian *et al*. 2015; Hendry *et al*. 2015) and lichens (Paukov *et al*. 2014; Favero-Longo *et al*. 2015). Although studies generally focus on the effects of a single stress factor, these stress factors are likely to have combined effects (Von Wettberg *et al*. 2014), as in the case for Ca : Mg ratio and water availability on traits of *Mimulus guttatus* (Phrymaceae, Murren *et al*. 2006; Selby *et al*. 2014). Presentations also focussed on elemental uptake and localisation in tissues of plants tolerant of ultramafic and other chemically imbalanced soils (Kosugi *et al*. 2015; Mizuno and Kirihata 2015; Pavlova *et al*. 2015), including the use of advanced techniques such as micro-PIXE in mapping regions of elemental concentration within plant tissue (Przybyłowicz *et al*. 2005, 2014). Tolerance of high concentrations of heavy metals, including molecular mechanisms underlying metal tolerance, has also received attention (Janssens *et al*. 2009; Gall and Rajakaruna 2013; Viehweger 2014). There has been considerable effort to understand the linkage between ultramafic-soil stress factors for plants (such as metals, nutrients, water) and the genes that underlie adaptations to them (Von Wettberg *et al*. 2014). Recent advances in molecular biology and genomics have provided powerful tools to examine the genetic bases for adaptation to ultramafic soils (Von Wettberg and Wright 2011; Selby *et al*. 2014). In *Arabidopsis*, for example, polymorphisms for traits involved in Ca : Mg tolerance and heavy-metal detoxification have been detected in ultramafic and non-ultramafic populations (Turner *et al*. 2008, 2010), suggesting that parallel ecological adaptations (Rajakaruna *et al*. 2003; Ostevik *et al*. 2012) can occur via the differentiation of the same polymorphism at ultramafic-tolerant loci in geographically distinct ultramafic-tolerant populations. An often used approach for identifying genes involved in ultramafic adaptation is the study of quantitative trait loci (QTL; Bratteler *et al*. 2006; Murren *et al*. 2006; Wu *et al*. 2008). Recent advances in various fields of molecular biology may allow for even newer approaches to studying ultramafic-plant physiology and the underlying genetics of adaptations (Von Wettberg and Wright 2011; Selby *et al*. 2014).

Ultramafic plants and their associated biota are also ideal model systems to explore the role of divergent natural selection in speciation (Rajakaruna 2004; Kay *et al*. 2011). Intraspecific variation is central to divergence. Population-level variation for adaptive traits, and traits that are responsible for reproductive isolation, is known to occur within ultramafic-tolerant species across distinct plant families (O'Dell and Rajakaruna 2011). Such intraspecific variation is highlighted in several studies in this Special Issue, including those by Burgess *et al*. (2015*b*), Chathuranga *et al*. (2015), McAlister *et al*. (2015) and Reeves *et al*. (2015). Research on ultramafic plants, including *Mimulus*, *Layia* (Asteraceae), *Collinsia* (Plantaginaceae), *Helianthus* (Asteraceae), *Noccaea* and *Lasthenia* (Asteraceae), have contributed greatly to our understanding of factors and mechanisms underlying speciation (Kay *et al*. 2011), demonstrating how edaphic specialisation can greatly reduce gene flow among divergent populations (via both pre- and post-zygotic reproductive barriers), setting the stage for subsequent speciation. Ecological approaches, including reciprocal-transplant and common-garden experiments, have often been employed to examine local adaptation (Bieger *et al*. 2014) and how ecological divergence can lead to reproductive isolation between closely related taxa (Wright and Stanton 2011; Yost *et al*. 2012). Moyle *et al*. (2012) showed that post-zygotic isolation via hybrid sterility can occur between adjacent ultramafic and non-ultramafic ecotypes, contributing to reduced gene flow and setting the stage for further genetic differentiation via edaphic specialisation.

Whether there is a cost associated with ultramafic tolerance has also been of interest in recent years. Studies suggest that ultramafic-tolerant plants are generally less competitive (see Anacker 2014) and more susceptible to herbivore or pathogen pressure (Lau *et al*. 2008) when found on non-ultramafic soils and that these biotic factors may drive edaphic specialisation. Whether the cost associated with specialisation is greater for endemics than for those only tolerant of ultramafic soil has not yet been tested using closely related species pairs or conspecific populations (Kay *et al*. 2011). Such studies could shed light on why some taxa become endemic to ultramafic soils, whereas others are found on and off ultramafics, seemingly indifferent to the 'harsh' substrate. The modes of origin for ultramafic endemics are also of interest (Harris and Rajakaruna 2009; Kay *et al*. 2011). Phylogenetic studies have suggested that, in some cases, the evolution of ultramafic endemism is rapid and local (forming neoendemic species, Anacker and Strauss 2014) and, in others, endemism is via biotype depletion (forming paleoendemic species, Mayer *et al*. 1994). Anacker *et al*. (2011) and Anacker (2011) have undertaken meta-analyses of molecular phylogenies to explore patterns of diversification on serpentine and the effects of evolutionary and biogeographic histories and regional environmental conditions on the origins of ultramafic endemism. Those analyses have shown that ultramafic endemics exhibit few transitions out of the endemic state, suggesting adaptation to ultramafic and subsequent edaphic restriction can lead to an evolutionary 'dead end.' Research by Kolár *et al*. (2012) and Ivalú Cacho *et al*. (2014), however, suggested that ultramafic lineages may not always represent evolutionary 'dead ends', but, rather, dynamic systems with a potential to further diversify via independent polyploidisation and hybridisation, even providing pathways to radiate off ultramafic soils.

Threats and conservation (Session 5)

In many ultramafic ecosystems worldwide, mining for Ni and other mineral resources contained within ultramafic regoliths presents a major threat to their biodiversity. Nowhere is this threat so dire as in New Caledonia, which is one of the world's most important biodiversity hotspots (Wulff *et al*. 2013). The mining industry is rapidly growing in New Caledonia, with the total production of Ni anticipated to triple in 2015 (Fogliani *et al*. 2014). The New Caledonian Agronomic Institute conducts research to assist in the protection of endangered species, specifically by identifying priority local hotspots and species. As an example, rare species such as *Callitris sulcata* (Cupressaceae) and *Araucaria rulei* (Araucariaceae), are the subject of ongoing population genetic and ecological studies so as to formulate effective species-management plans (Fogliani *et al*. 2014). Elsewhere, in the Philippines, the impact of Ni mining is minimised by establishing vegetation strips in the mined landscape that act as a barrier against soil erosion, as well as providing ecosystem corridors, as work in the Caraga Region demonstrates (Varela *et al*. 2014). These have been termed 'ecobelts' and aim to capture resident biodiversity in degraded areas to assist natural regeneration over time. In Brazil, iron ore mining threatens the unique vegetation of the 'Ironstone Outcrops' and an environmental-impact assessment recently concluded that four sites are now *Critically Endangered*, 11 are *Endangered*, 18 are *Vulnerable*, and only one is *Stable* (Jacobi *et al*. 2014). The negative impacts are anticipated to be even higher in the coming years as a result of habitat loss associated with opencast mining and the lack of officially protected areas.

In Sabah, where the 8th ICSE was held, no active mining for mineral resources is taking place at present. However, the greatest impact on ultramafic ecosystems results from forest clearing for the timber industry and for the establishment of palm oil plantations. In Sabah, 39.5% of the total forest area existing in 1973 had become deforested by 2010 (Gaveau *et al*. 2014) and protected areas amount to 8% of the land surface (Bryan *et al*. 2013). There are, however, several large protected areas that encapsulate important ultramafic ecosystems. These include Parks (managed by Sabah Parks) and Forest Reserves (managed by the Forestry Department).

In the United Sates, urban development in the San Francisco Bay Area also threatens the long-term viability of ultramafic ecosystems (US Fish and Wildlife Service 1998). Regulatory tools are being used there to balance urban development with conservation of the region's unique ultramafic-associated flora and fauna (Harris 2014). Detailed studies on the genetics and habitat requirements of coyote ceanothus (*Ceanothus ferrisiae*, Rhamnaceae), a rare shrub, have led to the identification of a suitable introduction site, to mitigate the impending threats to its largest population as a result of planned dam construction activities (Hillman *et al*. 2014).

Although not of ultramafic origin, the Copper–Cobalt Belt of the Democratic Republic of the Congo and Zambia is the richest globally for metallophytes and hyperaccumulators, with over 600 such species having been described (Malaisse 2014). Research undertaken by the universities of Lubumbashi, Liège and Brussels has led to the creation of an online database (www.copperflora.org, accessed 31 March 2015) and to an upcoming book entitled '*Copper-cobalt flora of Katanga and northern Zambia*'. Unfortunately, this unique ecosystem is under acute threat because many of the 'copper hills' are being mined and several species are already thought extinct (Malaisse 2014).

Although the rich biodiversity of many ultramafic ecosystems is often emphasised, limited research on these ecosystems has been undertaken in some of the most biodiverse regions of the world. For example, the ultramafic outcrops on the islands of Sulawesi and Halmahera in Indonesia, covering 15 400 km^2 and >5500 km^2, respectively, have hardly been studied (van der Ent *et al*. 2013*b*). Borneo Island has approximately 14 500 species of plants (Roos *et al*. 2004) and at least 4000 of these occur on ultramafic soils (van der Ent *et al*. 2015). Without adequate information, it is difficult to formulate conservation strategies and priorities, although given the ongoing habitat destruction, it is evident that many plant species are threatened. Another, very specific, threat to ultramafic ecosystems is brought about by lateritic Ni-mining activities, mainly in Indonesia, the Philippines and New Caledonia. These mining activities target Ni-rich ultramafic soils, which often host species-rich vegetation with a high percentage of endemic species. Species adapted to thrive on ultramafic soils offer rich genetic resources for mine-site rehabilitation after strip-mining, but are likely to be destroyed during the mining operations.

These global examples have highlighted that ultramafic ecosystems are under threat in many areas around the world. The combined forces of urbanisation, mineral extraction and conversion of forests to plantations cast a bleak forecast for the survival of many rare and endemic plant and other species. Although not frequently emphasised, the lack of scientific knowledge of the plant diversity and ecology of ultramafic outcrops in South-east Asia and other less explored parts of the world puts constraints on protecting this biodiversity, with many species having already disappeared unnoticed. This exemplifies the urgent need for more research to assist in the conservation of areas most under threat (Whiting *et al*. 2004). The potential effects of climate change may have a further impact on the survival of many species restricted to ultramafic soils (see Fernandez 2014, and references cited therein).

Diversity, systematics and taxonomy (Session 6)

Ultramafic outcrops are home to unique plant communities characterised by rare and endemic species (Kruckeberg 1984; Brooks 1987; Alexander *et al*. 2007; Rajakaruna *et al*. 2009; van der Ent *et al*. 2014*b*). Ultramafic outcrops are extensive in Sabah, covering an area of ~3500 km^2 and occur from sea level up to nearly 3000 m asl (Proctor *et al*. 1988; Repin 1998). Sabah is extremely biodiverse, with an estimated 8000 plant species (Wong 1992), of which at least 800 species are endemic (Maycock *et al*. 2012). In total, 4252 species have been recorded from the ultramafic soils in Sabah (van der Ent *et al*. 2014*a*). Within Sabah, Kinabalu Park is the pinnacle of plant diversity, with over 5000 plant species in an area <1200 km^2, the most species-rich area on Earth in terms of species density (Beaman 2005). In Kinabalu Park, ultramafic soils support at least 2854 plant species in 742 genera and 188 families (van der Ent *et al*. 2014*a*). Elsewhere in Sabah, there is remarkable diversity of insects in the ultramafic Tinkar Forest Reserve (Chung *et al*. 2014). Also, in the Sungai Imbak Virgin Jungle Reserve, 62 Dipterocarpaceae species from six genera were recorded, including 15 species as new records (Majapun *et al*. 2014). The biodiversity riches of ultramafic outcrops at Tawau Forest Reserve and in the Mount Silam Forest Reserve were also noted during the conference (Nilus *et al*. 2014; Pereira *et al*. 2014). The latter contained 282 taxa from 72 families; some are narrow endemics known only from that site. Elsewhere in Asia, remote-sensing studies were undertaken in the Andaman group of islands of India where supervised classification of the vegetation revealed three distinct outcrops in Rutland Island and on the hill top of Chidyatappu Island (Datta *et al*. 2014) and a dwarf scrub community on the top of the Saddle Hills in North Andaman Island (Chaudhury *et al*. 2014).

Taxonomic studies on *Cleisocentron* (Orchidaceae) and *Ternstroemia* (Pentaphylacaceae) revealed several species restricted to ultramafic soils in Sabah (Nyee-Fan *et al*. 2014; Sabran *et al*. 2014). Species of carnivorous pitcher plants in *Nepenthes* have attracted significant interest in Sabah (Clarke 1997), with 22 of the 39 Bornean *Nepenthes* found in Sabah (Damit *et al*. 2014). Kinabalu Park is the most species-rich (14 species); five species are endemic to Kinabalu Park, namely *N. burbidgeae*, *N. edwardsiana*, *N. rajah* and *N. villosa*. Detailed ecological studies in Kinabalu Park have shown that physiognomy, rather than co-occurring species composition, determines habitat differentiation of *Nepenthes* species (Sumail and Van der Ent 2014).

Elsewhere on the globe, the plant diversity of ironstone outcrops in south-eastern Brazil was highlighted by Jacobi *et al*. (2014). Also, in South Africa, in the vegetation of Griqualand, most endemic plants were edaphic specialists with a preference for specific geologic substrates; however, distribution modelling indicated that climate overrides edaphic preference in some instances (Frisby *et al*. 2014). Another study from South Africa focused on plant–soil relations of the Vredefort Dome (an impact structure) and how abrupt transitions in soil chemical characteristics can ultimately affect the floristic and physiognomic characteristics of the associated vegetation (Boneschans *et al*. 2015). Finally, ecological succession on Cu-contaminated mine tailings in the Philippines was reported to consist of *Digitaria sanguinalis*, *Paspalum conjugatum* and *P. scrobiculum* (all Poaceae) in the early stages, which are then replaced by *P. conjugatum*, *Cynodon dactylon* (Poaceae) and *Cuphea carthagenensis* (Lythraceae), with associated increases in soil pH and organic matter content (Cuevas and Balangcod 2014).

Summary

Ultramafic geoecology is now a significant focus in the natural sciences. A recent (20 February 2015) search on Web of Science (from all databases) of the topic 'serpentine and ecology' yielded 853 results with 8688 citing articles (without self-citations) over the past 20 years, with an exponential growth in citations during the past decade. Studies conducted in geology, pedology, microbiology, ecology, evolution, conservation and restoration of ultramafic ecosystems continue to unearth unresolved questions, setting the stage for multidisciplinary and interdisciplinary research worldwide. We have summarised some of the contributions made during the 8th International Conference on Serpentine Ecology held in Sabah, Malaysia and described some of the exciting challenges awaiting future research in this double issue (1–2 combined), and the next double issue (3–4 combined) of

Australian Journal of Botany. We hope that the 9th International Conference (scheduled for 2017 and hosted by The Agricultural University of Tirana in Albania) will be as successful as were the 8th (and prior) conferences in advancing our knowledge of ultramafic ecosystems worldwide.

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