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REVIEW

Copper endemism in the Congolese flora: a database of copper affinity and conservational value of cuprophytes

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Background and aims – The occurrence of natural plant communities on Cu-enriched substrates over significant areas of the earth's surface is exceptional. In Katanga (D.R.Congo), natural outcrops of copper-rich rocks are colonised by highly original plant communities. A number of plant species have been proposed as possibly endemic to those sites. Here we revise the taxonomic, phytogeographic and conservational status of these plants.
Methods – Almost all the herbarium materials of supposed Cu-endemics available in BR and BRLU have been revised and all relevant taxonomic revisions have been consulted. Literature and herbarium data have been supplemented by original observations in the field. Conservational status was established using IUCN criteria based on current and projected variation of population size and number.
Key results – Thirty-two taxa are identified as strict endemics of Cu-rich soil in Katanga, i.e. absolute metallophytes. Twenty-four of these are known from one to five localities only. Twenty-three other taxa are identified as broad endemics, i.e. with > 75% of occurrence on Cu-rich soil. Fifty-seven other names formerly used for supposed endemics are rejected either for nomenclatural or phytogeographic reasons. A number of species formerly regarded as endemics have been discovered off copper-enriched substrates due to progress in the botanical exploration of Katanga. The taxonomic value of a number of proposed endemics is still uncertain and requires further research. For a number of taxa, local geographic distribution still remains insufficiently known. The low proportion of endemics (c. 5%) in the flora of Cu-rich soil in Katanga possibly indicates a recent origin of much of this flora. Arguments in favour of neoendemism and relictual endemism, respectively, are discussed briefly. Ten percent of strict endemics are extinct and 65% are critically endangered, due to actual or projected habitat destruction by copper mining. Endemics restricted to primary habitats may be the most difficult to conserve. Several species, mostly annuals, are able to thrive on secondary metalliferous habitats created by the mining industry and may thus be at lower risk.
Conclusions – This review emphasizes the high conservation value of the flora of Cu-rich soil in Katanga and should help prioritise future conservation efforts.

Key words – metallophyte, endemic, copper, cobalt, Katanga, mining, heavy metals, conservation, D.R.Congo, threatened species.

INTRODUCTION

Plant populations established on geochemical anomalies often offer outstanding examples of ongoing microevolutionary processes due to geographical isolation, ecological isolation and stringent selective forces (Antonovics et al. 1971, Ernst 1974, Baker et al. 1992, Raven 1964, Kruckeberg 1984, 1986, Macnair & Gardner 1998, Rakajaruna 2004). In particular, metalliferous substrates often support highly distinctive plant communities including a number of endemic species (Duvigneaud & Denaeyer-De Smet 1963, Wild 1974, Kruckeberg 1984, Kruckeberg & Kruckeberg 1990, Brooks & Malaisse 1990, Jaffré 1992, Borhidi 1996, Rajakaruna & Bohm 2002). Evolutionary biologists have long been interested in the endemic flora of metalliferous substrates as a possible example of the relationships between adaptation and speciation (Stebbins 1942, Raven 1964, Stebbins & Major 1965, Ernst 1974, Kruckeberg 1984, Kruckeberg & Kruckeberg 1990, Wild & Bradshaw 1977). However, the speciation process in metalliferous habitats has been little studied (Brady et al. 2005). In addition, metallophytes species possess remarkable physiological adaptations required to grow on substrate enriched in heavy metals and are key materials to implement green technologies aimed at remediating heavy metal pollutions (Baker et al. 2000). The flora of metalliferous sites is therefore of high value to biodiversity conservation (Whiting et al. 2004).

Whereas serpentine soils have received much attention from an evolutionary and phytogeographic point of view (Wild 1965, 1974, Kruckeberg 1984, Jaffré 1992, Borhidi 1996, Rajakaruna & Bohm 2002, Reeves et al. 2007, Brooks 1987), other natural metalliferous substrates have been comparatively less well studied. Ecosystems established on soils naturally enriched with copper are of rare occurrence. SC Africa is exceptional in the occurrence of a large number of copper-cobalt mineralised areas (Duvigneaud & Denaeyer-De Smet 1963, Ernst 1974, Wild & Bradshaw 1977, Malaisse 1983, Brooks & Malaisse 1985, Leteinturier & Malaisse 1999, Leteinturier 2002). In the Katangan copper belt (D.R.Congo), Cu-rich rock outcrops are remarkable in the landscape in the form of isolated hillocks covered by steppic savannah which sharply contrasts with the surrounding miombo woodland (Duvigneaud & Denaeyer-De Smet 1963, Shewry et al. 1979, Brooks & Malaisse 1985). High concentrations of copper are most often associated with elevated concentrations of cobalt and other heavy metals. The Katangan copper belt has been recognised as a hotspot for metallophyte species (Wild & Bradshaw 1977, Brooks & Malaisse 1985, 1990, Malaisse 1983, Malaisse et al. 1983, Leteinturier & Malaisse 1999).

All over the world the flora of metalliferous soils is threatened by human activities, especially mining, and Katanga makes no exception. Actions aimed at preserving metallophyte species are imperative (Whiting et al. 2004). In Katanga, a dozen sites have already been completely destroyed and many others have been profoundly disturbed (Brooks et al. 1992).

Conservation strategies should be based upon a full appreciation of biogeographic originality and conservational value of a given flora. Such an appreciation must also rely on a sufficient taxonomic knowledge (Callmander et al. 2005). For a long time, botanists have relied on the seminal work of Duvigneaud for taxonomy, ecology and distribution of Katangan metallophytes (Duvigneaud 1958, Duvigneaud 1959, Duvigneaud & Denaeyer-De Smet 1960, Duvigneaud & Denaeyer-De Smet 1963) (see Leteinturier and Malaisse (2001) for a historical account of botanical exploration of copper soils in Katanga). Duvigneaud and Denaeyer-De Smet (1963) listed c. 250 species on copper sites and considered that the number of copper-endemics might be close to 100 species. More recent explorations (especially by F. Malaisse and co-workers) have steadily increased the number of species recorded to occur on copper-enriched-soil, which is now close to 600 (Leteinturier 2002, F. Malaisse personal obs.). New endemic species have been described (e.g. Robyns 1989, Malaisse & Lecron 1990). However, progress in the botanical exploration of Katanga has also revealed that taxa initially regarded as endemic actually had a broader range also occurring on normal soil. At the same time, taxonomic revisions have synonymised a number of taxa originally described by Duvigneaud as copper-endemics. In the last published reviews some forty species were cited as endemic to the copper habitat (Leteinturier 2002, Whiting et al. 2004). Due to a lack of synthesis of this information, the conservational status of Katangan copper species has not been assessed yet. This has precluded the inclusion of Katangan copper species in the IUCN Red List, a situation which may seriously undermine conservation efforts (for a discussion of appropriate uses of the Red List, see Possingham et al. 2002, Lamoreaux et al. 2003).

In this paper, we aim to establish an inventory of species endemic of copper-enriched soils in Katanga (D.R.Congo), and to assess their current distribution range and conservation. To that end, we critically revise the taxonomic status and ecogeographic distribution of virtually all taxa that have ever been reported to be endemic of copper-enriched soil in Katanga, based upon an extensive revision of the herbarium materials and relevant literature. We also provide a first assessment of their conservation status using the IUCN typology. The percentage of endemic species is compared to other floras of metal-enriched soil elsewhere on the earth and the possible origin of the endemic flora of copper-enriched soils in Katanga is discussed briefly.

MATERIALS AND METHODS

Geographical setting and climate

The "Katangan Copper Belt" (D.R.Congo) forms a crescent c. 300 km long and 50 km wide extending from Kolwezi in the west to Lubumbashi in the southeast of Katanga province. Mineralised rocks appear as rounded hills, typically a few tenths of meters above the level of the surrounding non mineralised areas. Most copper hills are typically a few tenths of hectares in area, rarely exceeding 1 km² (personal obs.). The distance between nearby hills varies enormously across the Copper Belt from less than a few hundred meters to more than 20 km. The total number of mineralised hillocks is not known precisely, but > 200 sites are recorded in the database of the Gécamines (personal obs.). Less than one hundred hills have been explored botanically on at least one occasion (Leteinturier et al. 1999, Leteinturier 2002).

The Katangan Group is of Upper Cambrian age (i.e. over 620 my old). It comprises three large series: Upper Kundelungu, Lower Kundelungu and Roan (François 1973). Copper mineralization in Katanga province is found in the Roan Series comprising calcareous rocks with dark minerals, dolomitic schist, cellular siliceous rocks, flaky siliceous rocks, stratified dolomites and argillaceous talc.

The climate is humid subtropical (Köppen-Geiger: CWa) and tempered by the relatively high elevation (c. 1300 m a.s.l.). There is one rainy season (November to March), one dry season (May to September) and two transition months (October and April). Annual rainfall is about 1300 mm of which 1200 mm fall during the rainy season. Mean annual temperature is about 20°C. Temperature is lowest at the beginning of the dry season (15–17°C). September and October are usually the warmest months with daily maxima of about 31–33°C.

Three sources of information have been used to construct a database: published literature, herbarium materials and unpublished field observations by the authors (often supported by a herbarium voucher specimen). First, a working list of putative endemics taxa was compiled based on all published papers on the flora of Katangan copper hills with explicit indications on plant affinity with copper soil (Robyns 1932, Duvigneaud 1958, Duvigneaud 1959, Duvigneaud & Denaeyer-De Smet 1960, Duvigneaud & Denaeyer-De Smet 1963, Malaisse 1983, Brooks & Malaisse 1990, Leteinturier & Malaisse 1999, Leteinturier 2002). All species that had been reported as endemic of or having high affinity for Cu-rich substrate by at least one of those authorities were considered. All species classified as "absolute cuprophytes", "local cuprophytes" and "cuprophiles" by Duvigneaud (loc. cit.) have been considered. The second step was to validate putative endemics. To that end, each species in the first list was critically assessed both from a taxonomic and phytogeographic point of view.

Nomenclatural and taxonomic revision

The following standard floras have been used: Flore d'Afrique centrale (Multiple authors 1948–1962; 1967–1971; 1972–1996; 1997–), Flora Zambesiaca (Multiple authors 1960–) and Flora of Tropical East Africa (Multiple authors 1952–). For taxa that have not been treated yet in these floras, the most recent taxonomic revisions and monographs for Central Africa have been used. In all cases, the protologue was consulted. The following electronic resources have also been used: Botany & Plant Science of ALUKA (http://www.aluka.org/action/showDiscipline?sa=bot), the International Plant Names Index (IPNI) (http://www.ipni.org), the African Flowering Plants Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/). The most recently accepted name has been retained. Some putative endemics were rejected because they have been synonymised with taxa with a broader distribution range of copper-enriched substrates. In a limited number of cases, different taxonomic revisions have expressed conflicting views as to the taxonomic value of some taxa occurring on Cu soil. Such cases will be examined in the discussion.

Phytogeographic revision

For all taxa taxonomically validated in the first list, the proportion of localities on Cu soil vs. non Cu soils was determined based on an extensive survey of published literature and herbarium collections. For all these species, virtually all herbarium materials kept in BR, BRLU, BRVU, GENT and Kipopo (Katanga) have been examined for location and ecology. More than 1900 herbarium specimens have been seen. Additional data came from our own observations (personal obs.), especially since 2005 and from the original field notes of P. Duvigneaud (kept in BRLU). Particular attention was paid to records of putative endemics on non Cu substrates (especially steppic savanna on Kalahari sands of the Katangan highlands ("Hauts-Plateaux katangais"), nonmetalliferous rock outcrops, lateritic crust, woodland miombo or other metalliferous habitats: Zn, Pb, Mn). Occurrence on Cu-enriched soil was accepted if it was explicitly mentioned on the herbarium label. In very few cases, occurrence on Cu soil was inferred from locality name (e.g. "Mine de l'Etoile") even if no explicit ecological data were recorded by the collector. Affinity for Cu soil was calculated as the proportion of records on Cu soil and categorised as follows: < 75%, 75–99%, 100%. Taxa with 100% of records on Cu soil are here regarded as strict endemics of Katangan copper soil (i.e. absolute metallophytes). Our definition of endemism is somewhat more restrictive than in the recent Californian serpentine database (Safford 2005) which accepted as serpentine endemics all species with > 95% locations on serpentine. A second list of broad endemics was established comprising species having > 75% of localities on Cu-soil and a few species with a total of only 3 known localities, two of which (66%) are on Cu soils.

Ecology of endemics

The habitat of each species was determined based on herbarium collections and published literature completed by our recent observations in the field. Three types of habitats have been distinguished. Primary habitats are natural, undisturbed plant communities, including steppic savannah, rocky steppe and scrub comprising mostly perennial species. Secondary habitats are substrates which have been disturbed by man. Two types of secondary habitats have been distinguished depending on the source of metallic contamination: i) mine deposits (mostly mineralised rock debris) disturbed by artisanal or industrial mining activities, ii) soil contaminated by atmospheric fallout from copper smelters (Mbenza et al. 1989).

IUCN red list status

The conservational status of strict and broad endemics was assessed using IUCN criteria in April 2008. In this assessment, the current or potential threats on populations were assessed as follows. Mining maps of Katanga province ("cadastre minier") allowed us to determine the status of the sites (i.e. currently mined, mining planned, no mining planned).

Table 1 – Plant taxa strictly endemic of Cu-rich soil in Katanga, D.R.Congo (absolute metallophytes), with their IUCN status, habitat and number of sites.
EX: extinct, CR: critically endangered, EN: endangered, VU: vulnerable, DD: data deficient. P: Primary habitats. S: Secondary habitats. S1: with substrate (often mine debris) disturbed and reworked by mining industry, S2: contaminated by atmospheric fallout from metal smelter.

Taxon (accepted name and synonyms)	**Family**	**Sites**	**IUCN red list status**	**Habitat**
Acalypha cupricola W.Robyns ex G.A.Levin	Euphorbiaceae	51	(EN B2a + 3d)	P, S1
Acalypha dikuluwensis P.A.Duvign. & Dewit	Euphorbiaceae	1	EX	P
Actiniopteris kornasii Medwecka-Kornas	Pteridaceae	4	(CR B2a+(b(i,ii,iii,iv)))	P
Aeollanthus saxatilis P.A.Duvign. & Denaeyer	Lamiaceae	4	(CR B2a+(b(i,ii,iii,iv)))	P
Basananthe cupricola A.Robyns	Passifloraceae	1	EX	P
Batopedina pulvinellata Robbr. subsp. *glabrifolia* Robbr.	Rubiaceae	4	(CR B2a+(b(i,ii,iii,iv)))	P
Bulbostylis fusiformis Goetgh.	Cyperaceae	3	(CR B2a+(b(i,ii,iii,iv)+(c(iii)))	P, S1
Cheilanthes inaequalis (Kunze) Mett. var. *lanopetiolata* P.A.Duvign. (*Notolaena inaequalis* Kunze var. *lanopetiolata* P.A.Duvign.)	Pteridaceae	1	(CR B1a+(b(i,ii,iii,iv)))	P
Commelina mwatayamvoana P.A.Duvign. & Dewit	Commelinaceae	2	(CR B2a+(b(i,ii,iii,iv)))	P
Commelina zigzag P.A.Duvign. & Dewit	Commelinaceae	5	(CR B1a+(b(i,ii,iii,iv)))	P, S1?
Crepidorhopalon perennis (P.A.Duvign.) Eb.Fisch. (*Lindernia perennis* P.A.Duvign.)	Scrophulariaceae	2	(CR B1a+(b(i,ii,iii,iv)+(c(iii)))	S1
Crotalaria cobalticola P.A.Duvign. & Plancke	Fabaceae	18	(EN B2a+(b(i,ii,iii,iv)))	P; S1
Crotalaria peschiana P.A.Duvign. & Timp.	Fabaceae	5	(CR B2a+(b(i,ii,iii,iv)))	P
Euphorbia cupricola (Malaisse & Lecron) Bruyns (*Monadenium cupricola* Malaisse & Lecron)	Euphorbiaceae	5	(CR B2a+(b(i,ii,iii,iv)))	P
Faroa chalcophila P.Taylor	Gentianaceae	3	(CR B2a+(b(iii,iv)+c(iii)))	S1
Faroa malaissei Bamps	Gentianaceae	11	(CR B2a+(b(i,ii,iii,iv)))	P
Gutenbergia pubescens (S.Moore) C.Jeffrey (*Gutenbergia cuprophila* P.A.Duvign.)	Asteraceae	2	(CR B2a+(b(i,ii,iii,iv)+(c(iii)))	S1
Hartliella cupricola Fischer	Scrophulariaceae	1	(CR B1a+(b(i,ii,iii,iv)))	P
Haumaniastrum robertii (Robyns) P.A.Duvign. & Plancke (*Acrocephalus robertii* Robyns)	Lamiaceae	32	(VU B1a+(c(iii)))	S1
Lopholaena deltombei P.A.Duvign.	Asteraceae	9	(CR B2a+(b(i,ii,iii,iv)))	P
Silene cobalticola P.A.Duvign. & Plancke	Caryophyllaceae	1	(CR B1a+(b(i,ii,iii,iv)))	P, S1?
Sopubia mannii Skan var. *metallorum* (P.A.Duvign.) Mielcarek (*Sopubia metallorum* P.A.Duvign.)	Orobanchaceae	9	(CR B2a+(b(i,ii,iii,iv)))	P
Triumfetta welwitschii Mast. var. *rogersii* (N.E.Br.) Brummitt & Seyani	Tiliaceae	DD	DD	P, S1?
Vernonia duvigneaudii Kalanda	Asteraceae	2	(CR B2a+(b(i,ii,iii,iv)))	P
Vernonia ledocteana P.A.Duvign. & Van Bockstal	Asteraceae	1	EX	P
Vigna dolomitica Wilczek	Fabaceae	1	(CR B2a+(b(i,ii,iii,iv)+(c(iii)))	S1
Wahlenbergia ericoidella (P.A.Duvign. & Denaeyer) Thulin (*Lightfootia ericoidella* P.A.Duvign. & Denaeyer)	Campanulaceae	3	(CR B2a+(b(i,ii,iii,iv)))	P
Wahlenbergia malaissei Thulin	Campanulaceae	2	(CR B2a+(b(i,ii,iii,iv)))	P
Requiring taxonomic re-evaluation (the last three not in Lebrun & Stork 1991, 1995)				
Cyanotis cupricola P.A.Duvign.	Commelinaceae	13	(EN B2a+(b(i,ii,iii,iv)))	P
Digitaria nitens Rendle subsp. *festucoides* P.A.Duvign.	Poaceae	1	DD	P
Loudetia kagerensis (K.Schum.) C.E.Hubb. subsp. *jubata* P.A.Duvign.	Poaceae	1	DD	P
Pandiaka metallorum P.A.Duvign. & Van Bockstal	Amaranthaceae	DD	DD	P, S1

Table 2 – Plant taxa with very high affinity to Cu/Co rich substrates in Katanga, D.R.Congo (broad endemics), with their IUCN status, habitat and number of sites.

Broad endemics: 75-99% of localities on Cu-soil in Katanga or a single locality on Cu-soil.

CR: critically endangered, EN: endangered, VU: vulnerable, DD: data deficient, NE: not evaluated. P: Primary habitats; S: Secondary habitats, S1: with substrate (often mine debris) disturbed and reworked by mining activities, S2: soil contaminated by atmospheric fallout from an ore-smelter.

Taxon	Family	Sites	IUCN status	Habitat
Ascolepis metallorum P.A.Duvign. & Léonard	Cyperaceae	29	(EN B2a+(c(iii)))	P, S1, S2?
Basananthe kisimbae Malaisse & Bamps	Passifloraceae	16	(EN B2a+(b(i,ii,iii,iv)))	P
Batopedina pulvinellata Robbr. subsp. *pulvinellata*	Rubiaceae	10	(EN B2a+(b(i,ii,iii,iv)))	P
Buchnera symoensiana Mielcarek (*Buchnera candida* P.A.Duvign. & Van Bockstal non S.Moore)	Orobanchaceae	3	(EN B1a+(b(i,ii,iii,iv)))	P
Bulbostylis cupricola Goetghebeur	Cyperaceae	36	(VU B1a+(c(iii)))	S1
Bulbostylis pseudoperennis Goetghebeur	Cyperaceae	24	(VU B1a+(c(iii)))	S1, S2
Cyperus kibweanus P.A.Duvign.	Cyperaceae	7	(CR B1a+(b(i,ii,iii,iv)))	P
Diplolophium marthozianum P.A.Duvign.	Apiaceae	10	(EN B2a+(b(i,ii,iii,iv)))	P
Dissotis derriksiana P.A.Duvign.	Melastomataceae	13	(EN B2a+(c(iii)))	P
Euphorbia fanshawei L.C.Leach	Euphorbiaceae	3	(EN B2a+(b(i,ii,iii,iv)))	P
Gladiolus ledoctei P.A.Duvign. & Van Bockstal (*G. fungurumeensis* P.A.Duvign. & Van Bockstal)	Iridaceae	16	(EN B2a+(b(i,ii,iii,iv)))	P
Gladiolus robiliartianus P.A.Duvign. (*Gladiolus duvigneaudii* Van Bockstal)	Iridaceae	8	(EN B1a+(b(i,ii,iii,iv)))	P, S1
Helichrysum lejolyanum Lisowski	Asteraceae	7	(VU B1a+(b(i,ii,iii,iv)))	P
Ipomoea linosepala Hallier f. subsp. *aureoargentea* P.A.Duvign. & Dewit	Convolvulaceae	6	(EN B2a+(b(i,ii,iii,iv)))	P
Justicia metallorum P.A Duvign.	Acanthaceae	26	(VU B1a+(b(i,ii,iii,iv)))	P
Ocimum ericoides (P.A.Duvign. & Plancke) A.J.Paton (*Becium ericoides* P.A.Duvign. & Plancke)	Lamiaceae	7	(EN B2a+(b(i,ii,iii,iv)))	P
Ocimum metallorum (P.A.Duvign. & Plancke) A.J.Paton (*Becium metallorum* P.A.Duvign. & Plancke)	Lamiaceae	DD	DD	P
Sopubia neptunii P.A.Duvign. & Van Bockstal	Orobanchaceae	17	(VU B1a+(b(i,ii,iii,iv)))	P
Thesium pawlowskianum Lawalrée	Santalaceae	3	DD	P
Tinnea coerulea Gürke var. *obovata* (Robyns & Lebrun) Vollesen (*Tinnea obovata* Robyns & Lebrun)	Lamiaceae	10	(VU B1a+(b(i,ii,iii,iv)))	P
Triumfetta likasiensis De Wild.	Tiliaceae	16	(VU B1a+(b(i,ii,iii,iv)))	P
Xerophyta demeesmaekeriana P.A.Duvign. & Dewit	Velloziaceae	DD	DD	P
Requiring taxonomic re-evaluation				
Ocimum monocotyloides (Plancke ex Ayob.) A.J.Paton (*Becium monocotyloides* Plancke ex Ayob.)	Lamiaceae	DD	DD	P
Monadenium pseudoracemosum Bally var. *pseudoracemosum* and var. *lorifolium* Bally	Euphorbiaceae	DD	DD	P

Personal observations in the field allowed us to assess current extent of habitat destruction and fragmentation. The main mining companies operating in Katanga agreed to communicate at least basic information about their operation plan schedule. Data from the ecogeographical revision have been combined with the current and predictable impacts of disturbance by mining activities to generate the Red List status of each taxon using IUCN (2001) criteria. B criterion was used to assess IUCN status using the geographic range in the form of either B1 (extent of occurrence) or B2 (area of occupancy). B1 and B2 were assessed by subcriteria a) and b) or c) by examining decline, fluctuations, fragmentation of populations and of occurrence and of occupancy area.

RESULTS

The inventory (tables 1–3)

Strict endemics – Thirty-two taxa (26 species, three subspecies, three varieties) are confirmed as strict Katangan Cu-endemics, i.e. with 100% of records on Cu-soil in Katanga (table 1). Ten of these (30%) are known only from the type locality. Only seven are known from > 10 localities. For four

Table 3 – Names formerly used for supposed Cu-endemics in Katanga not validated in the present study.
Taxa were rejected for one or several of the following three reasons: 1) taxon discovered off copper and with < 75% populations on copper soil; for such taxa, distribution range is given; 2) taxon merged with a broadly distributed species; 3) name rejected (unpublished name or nomen nudum). K = Katanga; BC = Bas-Congo; ZA = Zambia; AO = Angola; TZ = Tanzania; RW = Rwanda; MI = Malawi; ZI = Zimbabwe; MZ = Mozambique; TA tropical Africa.

Taxon	Accepted name (if different)	Family	Distr. range	Reference
Acrocephalus katangensis S.Moore	*Haumaniastrum katangense* (S.Moore) P.A.Duvign. & Plancke	Lamiaceae	K-ZA-TZ-AO	Paton & Brooks 1996
Aeollanthus rosulifolius P.A.Duvign. & Denaeyer	*Aeollanthus homblei* De Wild.	Lamiaceae	K	Ryding 1986
Anisopappus davyi S.Moore		Asteraceae	TA, ZA, K	Ortiz et al. 1996
Aspilia eylesii S. Moore subsp. *cupricola* P.A.Duvign. & Danhier	*Melanthera albinervia* O.Hoffm. subsp. *caudata* Wild	Asteraceae	TA	Beentje et al. 2005, this work
Barleria variabilis Oberm.	*Barleria descampsii* Lindau	Acanthaceae	K-ZA	Balkwill & Balkwill 1997
Becium aureoviride P.A.Duvign.	*Ocimum vanderystii* (De Wild.) A.J.Paton	Lamiaceae	K-ZA	Paton 1995
Becium aureoviride subsp. *lupotoense* P.A.Duvign.	*Ocimum vanderystii* (De Wild.) A.J.Paton	Lamiaceae	K-ZA	Paton 1995
Becium empetroides P.A.Duvign.	*Ocimum ericoides* (P.A.Duvign. & Plancke) A.J.Paton	Lamiaceae	K	Paton 1995, Paton et al. 1999
Becium grandiflorum (Lam.) Pic.Serm. var. *ericoides* (P.A.Duvign. & Plancke) Sebald	*Ocimum ericoides* (P.A.Duvign. & Plancke) A.J.Paton	Lamiaceae	K	Paton 1995, Paton et al. 1999
Becium homblei (De Wild.) P.A.Duvign. & Plancke	*Ocimum centrali-africanum* R.E.Fr.	Lamiaceae	K-ZA-TZ	Paton 1995
Becium metallorum P.A.Duvign. & Plancke	*Ocimum metallorum* (P.A.Duvign. & Plancke) A.J.Paton	Lamiaceae	K	Paton 1995
Becium peschianum P.A.Duvign. & Plancke	*Ocimum metallorum* (P.A.Duvign. & Plancke) A.J.Paton	Lamiaceae	K	Ayobangira 1987 Paton et al. 1999
Buchnera candida P.A.Duvign. & Van Bockstal non S.Moore	*Buchnera symoensiana* Mielcarek	Orobanchaceae		Mielcarek 1996 Malaisse et al. 1997
Buchnera cupricola Robyns	*Buchnera henriquesii* Engl.	Orobanchaceae		Mielcarek 1996, Malaisse et al. 1997
Buchnera duvigneaudii Malaisse	*Buchnera symoensiana* Mielcarek	Orobanchaceae		Mielcarek 1996, Malaisse et al. 1997
Buchnera metallorum P.A.Duvign. & Van Bockstal		Orobanchaceae	K	Mielcarek 1996, Malaisse et al. 1997
Buchnera robynsii Mielcarek **syn. nov.**	*Buchnera metallorum* P.A.Duvign. & Van Bockstal	Orobanchaceae	K	Mielcarek 1996, Malaisse et al. 1997
Buchnera rubriflora P.A.Duvign. & Van Bockstal	*Buchnera trilobata* Skan	Orobanchaceae	K-ZA-TZ-MI	Philcox 1990 Malaisse et al. 1997
Cheilanthes aff. perlanata sp. ined.	unpublished	Pteridaceae		Leteinturier (2002)
Chlorophytum linearifolium Marais & Reilly **syn. nov.**	*Chlorophytum colubrinum* (Baker) Engler	Anthericaceae	TA	This work
Cyphia gamopetala P.A.Duvign. & Denaeyer		Lobeliaceae	K	Thulin 1985
Dasystachys pulchella P.A.Duvign. & Dewit **syn. nov.**	*Chlorophytum colubrinum* (Baker) Engler	Anthericaceae	TA	This work
Eragrostis dikuluwensis P.A.Duvign. & Jacobs	Nomen nudum	Poaceae		
Eriospermum abyssinicum Baker	*Eriospermum flagelliforme* (Baker) J.C.Manning	Eriospermaceae	TA	Whitehouse 1996
Gladiolus actinomorphanthus P.A.Duvign. & Van Bockstal		Iridaceae	K	Thulin 1983
Gladiolus peschianus P.A.Duvign. & Van Bockstal	*Gladiolus tshombeanus* P.A.Duvign & Van Bockstal	Iridaceae	K	Geerinck 2005
Gladiolus tshombeanus P.A.Duvign. & Van Bockstal subsp. *parviflorus* P.A.Duvign. & Van Bockstal	*Gladiolus tshombeanus* P.A.Duvign & Van Bockstal	Iridaceae	K	Geerinck 2005

Table 3 (continued) – Names formerly used for supposed Cu-endemics in Katanga not validated in the present study.

Taxon	Accepted name (if different)	Family	Distr. range	Reference
Icomum albocandelabrum P.A.Duvign. & Denaeyer	*Aeollanthus homblei* De Wild.	Lamiaceae	K	Ryding 1986
Icomum biformifolium De Wild.	*Aeollanthus subacaulis* (Baker) Hua & Briq. var. *linearis* (Burkill) Ryding	Lamiaceae	K-BC-ZA-TZ	Ryding 1986
Icomum elongatum De Wild.	*Aeollanthus subacaulis* (Baker) Hua & Briq. var. *linearis* (Burkill) Ryding	Lamiaceae	K-BC-ZA-TZ	Ryding 1986
Icomum lineare Burkill	*Aeollanthus subacaulis* (Baker) Hua & Briq. var. *linearis* (Burkill) Ryding	Lamiaceae	K-BC-ZA-TZ	Ryding 1986
Icomum tuberculatum De Wild.	*Aeollanthus subacaulis* (Baker) Hua & Briq. var. *ericoides* (De Wild.) Ryding	Lamiaceae	K	Ryding 1986
Ipomoea alpina Rendle subsp. *argyrophylla* P.A.Duvign. & Dewit	*Ipomoea linosepala* Hallier f. subsp. *alpina* (Rendle) Lejoly & Lisowski	Convolvulaceae	K-ZA-BY-TZ-AO	Lejoly & Lisowski 1992
Ipomoea alpina Rendle subsp. *hirsutula* P.A.Duvign. & Dewit	*Ipomoea linosepala* Hallier f. subsp. *alpina* (Rendle) Lejoly & Lisowski	Convolvulaceae	K-ZA-BY-TZ-AO	Lejoly & Lisowski 1992
Ipomoea alpina Rendle subsp. *hockii* (De Wild.) P.A.Duvign. & Dewit	*Ipomoea linosepala* Hallier f. subsp. *alpina* (Rendle) Lejoly & Lisowski	Convolvulaceae	K-ZA-BY-TZ-AO	Lejoly & Lisowski 1992
Ipomoea alpina Rendle subsp. *longissima* P.A.Duvign. & Dewit	*Ipomoea linosepala* Hallier f. subsp. *alpina* (Rendle) Lejoly & Lisowski	Convolvulaceae	K-ZA-BY-TZ-AO	Lejoly & Lisowski 1992
Ipomoea debeerstii De Wild. subsp. *discolor* P.A.Duvign	*Ipomoea recta* De Wild.	Convolvulaceae	K-ZA-MI	Lejoly & Lisowski 1992
Ipomoea linosepala Hallier f. subsp. *auroargentea* P.A.Duvign. & Dewit		Convolvulaceae	K	Lejoly & Lisowski 1992
Justicia aff. *cupricola* sp. ined.	unpublished	Acanthaceae		Leteinturier (2002)
Karina tayloriana Boutique		Gentianaceae	K	Boutique 1972
Lapeirousia erythrantha (Klotzsch ex Klatt) Baker var. *welwitschii* (Baker) Marais ex Geerinck	*Lapeirousia erythrantha* (Klotzsch ex Klatt) Baker var. *setifolia* (Harms) Geerinck et al.	Iridaceae	K-MI-ZI	Goldblatt 1990
Lindernia damblonii P.A.Duvign.	*Crepidorhopalon tenuis* (S.Moore) Eb.Fisch.	Scrophulariaceae	K-ZA-TZ-BY-ZI	Fischer 1999
Ocimum homblei De Wild.	*Ocimum centraliafricanum* R.E.Fr.	Lamiaceae		Paton 1995
Ocimum katangense Robyns & Lebrun	*Ocimum centraliafricanum* R.E.Fr.	Lamiaceae		Paton 1995
Olax obtusifolia De Wild.		Olacaceae	K-ZA-TZ-MI-MZ	Lucas 1968
Pandiaka carsonii var. *carsonii* “écophénotype cupricole”	unpublished	Amaranthaceae	K-ZA-MI-ZI	Leteinturier (2002)
Pellaea aff. *pectiniformis* sp. ined.	unpublished	Pteridaceae		Leteinturier (2002)
Rendlia cupricola P.A.Duvign.	*Microchloa altera* (Rendle) Stapf.	Poaceae	K-SF	Cope 1999
Silene burchellii Otth. ex DC. “écophénotype cupricole”	unpublished	Caryophyllaceae		
Sporobolus deschampsioides P.A.Duvign.	*Sporobolus subulatus* Hack. ex S.Elliot	Poaceae	TA	Clayton et al. 1974
Sporobolus stelliger P.A.Duvign. & Kiwak	*Sporobolus congoensis* Franch.	Poaceae	TA	Clayton et al. 1974
Streptocarpus rhodesianus S.Moore var. *perlanatus* P.A.Duvign.	*Streptocarpus rhodesianus* S.Moore	Gesneriaceae	K-ZA-AO	Hilliard & Burtt 1971
Triumfetta cupricola De Wild.	*Triumfetta digitata* (Oliv.) Sprague & Hutch.	Tiliaceae	K-ZA-AO-BY-RW	Wilczek 1963
Triumfetta robynsii De Wild.	*Triumfetta dekindtiana* Engl.	Tiliaceae	K-ZA-TZ-BY	Wilczek 1963
Uapaca robynsii De Wild.		Euphorbiaceae	K-ZA-MI	Radcliffe-Smith 1996
Xerophyta barbarae subsp. *cuprophila* P.A.Duvign. & Dewit	*Xerophyta equisetoides* Baker var. *trichophylla* (Baker) L.B.Sm. & Ayensu	Velloziaceae	K-ZA-TZ-MI-ZI	Smith & Ayensu 1974
Xerophyta barbarae P.A.Duvign. & Dewit	*Xerophyta equisetoides* Baker var. *trichophylla* (Baker) L.B.Sm. & Ayensu	Velloziaceae	K-ZA-TZ-MI-ZI	Smith & Ayensu 1974

taxa (*Cyanotis cupricola*, *Digitaria nitens* subsp. *festucoides, Loudetia kagerensis* subsp. *jubata, Pandiaka metallorum*), little information is available apart from the protologue and we feel that their taxonomic value needs critical re-evaluation. Two of these are known only from the type specimen (*Digitaria nitens* subsp. *festucoides, Loudetia kagerensis* subsp. *jubata).*

Broad endemics – Twenty-four taxa (21 species, two subspecies, one variety) have > 75% of their localities on Cu-soil in Katanga and can be referred to as broad endemics (table 2). This group comprises a few absolute metallophytes not restricted to Cu-soil also occurring on other types of mineralised substrates (e.g. *Ascolepis metallorum* also on Zn/Pb and Mn-rich soil). *Bulbostylis cupricola* is actually restricted to Cu-soil, but its distribution range extends to the copperbelt of Zambia and it is thus not an endemic of D.R.Congo. The other broad endemics have a few occurrences (sometimes a single) on non-metalliferous soil. In many cases, these "odd" localities are not situated close to Cu-sites, most often occurring in the steppic vegetations of Katangan Highlands on Kalahari sands ("Hauts Plateaux katangais"). Most of these broad endemics are known from 10 localities or more. For two species (*Ocimum monocotyloides, Monadenium pseudoracemosum*) the taxonomic status of collections from Cu-soil is unclear and requires further research. For *Ocimum metallorum* and *Xerophyta demeesmaekeriana*, recent distributional data are insufficient.

Rejected taxa – Fifty-eight other names which had been previously used for supposed Katangan Cu-endemics by at least one literature reference are rejected here for one or several of the following reasons (table 3). First, a number of supposed endemics of low taxonomic value have been merged with taxa with a broader distribution range (e.g. *Xerophyta barbarae* synonymised with the widespread *X. equisetoides*). A second group comprises valid taxa which have been discovered in a relatively large number of sites on non mineralized soil (e.g. *Gladiolus tshombeanus*). Finally, a number of names are *nomina nuda* or have never been published. It should be noted that some of the "rejected endemics" are particularly frequent in Cu-vegetations (e.g. *Uapaca robynsii, Gladiolus tshombeanus, Aeollanthus subacaulis, …*).

Regional Cu-indicators – A distinct group comprises species with < 75% of their localities on Cu-soil when considering their whole distributional range, though occurring (almost) exclusively on Cu-soil in the Katangan copperbelt. These can be referred to as "regional Cu-indicators" ("local metallophytes" in Duvigneaud & Denaeyer-De Smet (1963)). Some of the most characteristic of these include *Anisopappus davyi*, *Microchloa altera*, *Crepidorhopalon tenuis*, *Haumaniastrum katangense.*

Ecology

Of the 32 strict endemics, 25 occur solely in primary communities. Three occur in primary communities and secondary communities on reworked substrate (*Acalypha cupricola*, *Crotalaria cobalticola*, *Bulbostylis fusiformis;* possibly also *Commelina zigzag* and *Silene cobalticola*) and five species (*Haumaniastrum robertii, Crepidorhopalon perennis, Vigna dolomitica, Gutenbergia pubescens, Faroa chalcophila*) are currently known only (or with few exceptions) from secondary communities on reworked mine debris, old mine tailings or otherwise disturbed substrates (table 1).

Of the 24 broad endemics, twenty apparently occur only in primary communities when present on copper-enriched soils, two occur in both primary and secondary communities and two species apparently only in secondary communities on disturbed substrate (*Bulbostylis cupricola, B. pseudoperennis*) (table 2).

IUCN status

IUCN red list status has been determined for 47 of the 58 (strict + broad) endemics. Of the "strict endemics", three species are extinct (*Acalypha dikuluwensis*, *Basananthe cupricola*, *Vernonia ledocteana*), 21 taxa are critically endangered, three are endangered, one is vulnerable and four are data deficient (table 1). Of the broad endemics, one is critically endangered, twelve are endangered, six are vulnerable, and five are data deficient (table 2).

DISCUSSION

Taxonomic difficulties

Thirty-one taxa (26 species, two subspecies and three varieties) are strict endemics of Cu/Co soil in Katanga. This number is much smaller than the estimation of c. 100 endemics proposed by Duvigneaud & Denaeyer-De Smet (1963: 216). This discrepancy has two explanations. Firstly, due to improved botanical exploration of Katanga many supposed endemics have eventually been found on normal soil. Secondly, recent taxonomic revisions have often used a broader species concept than that of Duvigneaud. Many taxa described by Duvigneaud from copper soil are now considered as having low taxonomic value (Ernst 1974). Many species in the Katangan copper flora show extensive morphological variation, with vicariant morphotypes occurring in different hills. Some of the most remarkable local variants on Cu-soil were given formal taxonomic recognition by Duvigneaud and co-workers (e.g. in the genera *Ocimum, Gladiolus, Pandiaka, Ipomoea, …*). Duvigneaud himself (loc. cit.) admitted that endemism on copper soil was mostly expressed at low taxonomic rank. However, the taxonomic treatment of many genera remains controversial. The genus *Ocimum* (= *Becium*) (Lamiaceae) offers a striking example. Sebald (1989) argued that the Cu-endemics described by Duvigneaud should best be treated as varieties of a single polymorphic taxon (*Ocimum grandiflorum*). A few years later, however, Paton (1992, 1995) expressed opposing views, arguing that species rank was more appropriate. Lebrun & Stork (1997) followed Sebald (1989). The Katangan copper flora offers a striking example of the influence of the species concept on conservation strategies (Agapow et al. 2004, Isaac et al. 2004). Irrespective of taxonomic implications, it is clear that the Katangan copper flora offers outstanding examples of microevolution at work, which should be investigated with molecular tools.

Table 4 – Endemism of metalliferous outcrops: comparison of six regions.
For each region, factors that might influence percentage of endemics are reported.

Metalliferous area	Number and proportion of endemic taxa (%)	Floristic richness	Elevational range (m)	Annual rainfall (mm)	Range and mean annual T°C	Age of outcrops	Last major palaeoclimatic event / vegetational change
Katangan Copper belt (D.R.Congo) (Cu-Co))	32 spp. – 5% (this study)	600	1200–1500	1300	5–33 (mean 20)	1–3 my (Decrée & Yans pers. comm.)	-18000 (Holocene): drier and colder (Vincens 1991)
Zimbabwean Great Dyke (Ni)	29 spp. – 7% (Wild 1978)	350	1100–1520	818	13–32	Not estimated	-18000 (Holocene): drier and colder (Vincens 1991)
New Caledonia (Ni)	1272 spp. – 69% (Jaffré 1992)	1844	1600	3000	10–30 (mean 20)	70 to 1 my (Harrison et al. 2004)	-30000 (Pleistocene) Fire and cyclone (Hope & Pask 1998, Hope & Tulipe 1994)
Cuba (Ni)	920 spp. – 66% (Borhidi 1996)	1400	300–1100	1192 (higher in mountain)	19–26 (mean 25)	30 my (eastern and western ends) 1 my (central island)	Dry period in Miocene and Pleistocene (-30000) (Borhidi 1996)
California (USA) (Ni)	176 spp. – 24% (Kruckeberg 1984)	727	2750	380–1300	15–30 (mean 22)	Miocene 25 to 5 my (Coleman and Kruckeberg (1999))	Onset of Mediterranean climate 5 my -30000 (Pleistocene)
Tuscany (Italy) (Ni)	25 spp. – 29% (Selvi 2007)	87	450–1700	800	10–30 (mean 20)		Onset of Mediterranean climate 5 my -30000 (Pleistocene)

Low proportion of strict endemics

The proportion of endemic species in the flora of the Katangan copper belt cannot be calculated precisely, because the total number of species is not known precisely. Duvigneaud & Denaeyer-De Smet (1963) recorded c. 230 species on Cu-soils, whilst Leteinturier (2002) listed 538 species. This number is still increasing as botanical exploration improves (personal obs.). Based upon a rough estimation of c. 600 species, the proportion of strict endemics is in the order of 5% (32/600).

How does this figure compare with the proportion of endemics in other metallicolous floras (table 4)? Serpentine soil in Cuba and New Caledonia, being oceanic islands with a long history of geographical isolation are admittedly not much relevant to the comparison. Serpentine soil in California and Italy have 23% and 29% of endemics, respectively, i.e. much higher values compared to Katanga.

What therefore can explain the relatively low proportion of endemic species in Katangese Cu-enriched soils? Age of exposure is an important factor to explain proportion of endemics in geochemical anomalies (Harrison et al. 2004). Copper mineralization in Katanga dates from late Cambrian (c. 620 my (François 1973)). However, Cu-rich rocks have been exposed to plant colonization for a much shorter period. Recent data indicates 2–3 my as a likely age for Katangese Cu outcrops (S. Decrée & J. Yans personal comm.). This figure is similar to the age of exposure of Californian serpentine outcrops with the lowest percentages of endemics (Harrison et al. 2004). Vegetation disturbance due to palaeoclimatic changes may also be relevant. During the Holocene, tropical Africa experienced dramatic climate fluctuations, including a dry-cool period c. 18,000 y BP (Scott 1984, Van Zinderen et al. 1988, Vincens 1991, Campbell et al. 1996). Therefore, much of the steppic flora may have recolonised copper hills when climate became warmer and moister, and before miombo forest eventually occupied most of upper Katanga (Scott 1984, Vincens et al. 2003, Vincens et al. 2005). Evolutionary divergence between populations isolated on the copper hills may therefore be recent, thus explaining the low percentage of endemic species. Significantly, the Zimbabwean Great Dyke (serpentine), which may have similar palaeoclimatic history as Katanga also has a low percentage of endemics (7%).

Another factor that may also account for the low proportion of endemism is the relatively low total area of mineralised soils in Katanga. Based on a typical site area of a few tenths of hectares the total area of the copper habitat may not exceed 100 km². This is at least one order of magnitude lower compared to the thousands of km² of serpentine soil existing in California, Italy, Cuba or New Caledonia (Brooks 1987).

Finally, ecological isolation and selective forces acting upon plant populations on Cu-enriched soil may have been overestimated. Contrary to serpentine soil, Katangan Cu-soils are relatively rich in nutrients (P, Ca, Mg) (Faucon et al. 2009b) and Cu toxicity may be mitigated by interactions with other metals in the soil (Faucon et al. 2009a). This might also explain the lower rates of evolutionary divergence between populations on Cu-soils and their counterparts on normal soil.

The case for neoendemism

Many if not all endemic species have close relatives on normal soil with a broader Zambezian distribution (Brooks & Malaisse 1985). Few if any endemic species appear to be taxonomically very isolated. A number of recent taxonomic revisions have emphasized the close morphological resemblance between a number of Cu-endemics and their more widespread counterparts (e.g. *Vigna dolomitica* and *V. reticulata* (Maxted et al. 2004); *Crotalaria peschiana* and *C. subcaespitosa* (Polhill 1982); *Acalypha cupricola* and *A. fuscescens*; *A. dikuluwensis* and *A. clutioides* (Levin et al. 2007); *Silene cobalticola* and *S. burchellii* (Malaisse et al. 1983)). Interestingly, *S. burchellii* possesses a copper ecotype which is intermediate between *S. burchellii* (on normal soil) and the narrow endemic *S. cobalticola* for both morphology and copper tolerance (Baker et al. 1983, Brooks & Malaisse 1985). This situation may indicate a derivative/progenitor relationship and a scenario of recent speciation in conditions of strong ecological isolation (Kruckeberg 1986, Macnair & Gardner 1998, Rajakaruna 2004, Rajakaruna & Whitton 2004).

Strict endemic species which occur (almost) only in secondary, man-made habitats (reworked debris and mine deposits) may conceivably have a (very) recent origin. Two of the most striking examples are *Haumaniastrum robertii* (related to *H. katangense)* and *Crepidorhopalon perennis* (related to *C. tenuis)*. Molecular tools should be used to test if these species have recently diverged from their counterparts in the new habitats created by mining activity. Of note is that *Mimulus cupriphilus*, the only copper endemic outside SC Africa, has been shown to be a recently evolved species of copper mines in California (Macnair 1988, Macnair & Gardner 1998). Morphological vicariance among populations of the same species in different sites also suggests that active speciation processes may be at work in the Katangan copperbelt. This observation also supports the hypothesis that many, if not all, copper endemics may qualify as neoendemics (Malaisse 1983, Brooks & Malaisse 1985, Brooks & Malaisse 1990). Evolutionary divergence between endemic metallophytes and their broader distributed counterparts should be investigated with molecular tools.

Relictual endemism?

For most broad endemics, populations off copper soil are located in steppic savannahs on Kalahari sands on the Katangese highlands ("Hauts-Plateaux katangais"), i.e. often more than 100 km away from the copperbelt. This suggests that some of the endemic species of the Copperbelt are relictual endemics, i.e. species that were once more widespread when steppic savannahs occupied most of Katanga (Duvigneaud & Denaeyer-De Smet 1963, Malaisse 1983, Brooks & Malaisse 1985) and which have been fragmented by forest expansion during the Holocene.

Ecology of endemics

Katangan copper hills are ecologically complex, encompassing a broad range of habitats (Duvigneaud & Denaeyer-De Smet 1963). In particular, they comprise natural habitats that are poorly represented on non mineralised substrates in Katanga, including rocky, non forested habitats (Duvigneaud 1958). Those rocks typically occupy the top of copper-hills and harbour a distinctive flora, rich in chasmophytic species. However, as most these rocks have been strongly leached by rain, their copper content within rooting depth is most often low (Duvigneaud & Denaeyer-De Smet 1963). Therefore, a number of species restricted to copper hills may not be highly metal tolerant and are actually not genuine metallophytes (*e.g. Aeollanthus saxatilis* and *Dissotis derriksiana*), a fact already acknowledged by Duvigneaud & Denaeyer-De Smet (1963).

Conservation

The endemic copper flora of Katanga is obviously at risk. Sixty-seven percent of endemic taxa qualify as critically endangered and 9% are already extinct (fig. 1). It is clear that conservation efforts should not be focused solely on strict

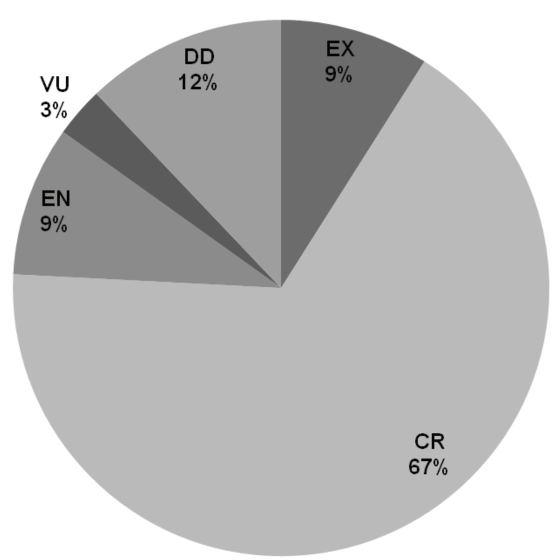

Figure 1 – Frequency distribution of IUCN categories of plant taxa strictly endemic of Cu-rich soil in Katanga. EX: extinct, CR: critically endangered, EN: endangered, VU: vulnerable, DD: data deficient

endemics. Species of interest to conservation should also include the broad endemics as defined in this work i.e. species with more than 75% of their populations in the copperbelt. Mining is the sole anthropogenic cause of extinction at present. Twelve copper hills have already been totally destroyed and c. forty (i.e. 50% of sites botanically explored) have been profoundly altered (Leteinturier 2002, Meersseman unpublished results). The steady increase of copper price on international markets between 2000 and 2008 has prompted new investments in the mines and an increasing number of sites are being destroyed rapidly, though market versatility may provide some respite.

Different ecological groups have to be distinguished among endemic species, which may require different conservation strategies. A first group comprises long-lived, slow growing species (mostly geophytes, geofrutex and chamaephytes) restricted to primary steppic savannah communities (*Loudetia-Cryptosepalum* steppic savannah and *Xerophyta* stone-packed steppe in Duvigneaud & Denaeyer-De Smet 1963) associated to stabilised substrates and with low colonization ability. Those species are not able to rapidly colonise recent mine debris and are thus highly vulnerable to habitat destruction by surface mining. Conservation of intact plant communities is arguably the best option for such species. Ex situ conservation is probably most difficult, requiring ecosystem reconstruction including translocation of substantial amounts of undisturbed topsoil.

A second group mostly comprises annal species occurring in pioneer open communities. These species can rapidly colonize the new substrates (mining debris and barren mineral areas, tailings) created by mining activities or soil contaminated by atmospheric fallout in the vicinity of metal smelters. A number of those species (e.g. *Crepidorhopalon tenuis*) are actually expanding their range on the huge areas of mine debris recently reworked by mining (Faucon et al. 2009b). These examples suggest that IUCN criteria for the establishment of conservation status of threatened species could be refined by taking into account the ability to colonize anthropogenic habitat. Those species may be easier to conserve in secondary habitats or in restored communities on reworked mineralized substrates. In other metallicolous habitats, it has been shown that specialised species may colonize secondary man-made habitats (Bizoux et al. 2004) and, even, exhibit higher fitness on those secondary habitats (Bizoux et al. 2008, Faucon et al. 2009b). Translocation of seed should be attempted in particular for *Bulbostylis fusiformis*, *Crepidorhopalon perennis*, *Crotalaria cobalticola*, *Faroa chalcophila*, *Gutenbergia pubescens*, *Haumaniastrum robertii* and *Vigna dolomitica*. Why some of these early successional species have such a narrow distribution range (e.g. one site for *Gutenbergia pubescens* and *Crepidorhopalon perennis*) is unclear (restricted dispersal or niche constraints) and merits investigation.

Need for further taxonomic and phytogeographic research

The Katangan copper flora is still insufficiently known. Firstly, it is significant that a number of taxa in our list are known only from the type specimen and a mention in Duvigneaud & Denaeyer-De Smet (1963). Some of them may be genuinely rare, but others may have been overlooked by recent collectors. Secondly, improved exploration has allowed describing several new endemic species in the last decades. Nine strict endemics have been described after Duvigneaud's work. Much herbarium material has been collected in the Katangan Copperbelt over the last decade especially by one of us (FM). This material may include new taxa still awaiting description. Conversely, for the same reason, several species previously thought to be strict copper endemics have been discovered off copper. Thirdly, biosystematic studies are badly needed to clarify the complex taxonomy of many genera in the Zambezian region (e.g. *Ocimum*: Sebald 1989, Paton 1995). Taxonomic difficulties are greatest for genera and families for which recent systematic revisions are lacking for D.R.Congo (e.g. Acanthaceae, Amaranthaceae, Anthericaceae, Commelinaceae, Cyperaceae, Lamiaceae, Poaceae) and with much herbarium materials unidentified to date (P. Meerts personal obs.).

CONCLUSIONS

The occurrence of natural copper-enriched substrates colonised by natural plant communities over significant areas is exceptional on the earth's surface. In Katanga 32 taxa are strict endemics of such habitats, and the Katangan copper hills offer striking examples of ongoing microevolutionary processes. Our phytogeographic and taxonomic revision represents a step for the conservation of Congolese copper flora. However, biosystematic and molecular-based studies are urgently needed to clarify phylogenetic relationships between Cu-endemics and related species, explore phylogeographic scenarios and reconsider species limits.

Most endemics qualify as critically endangered. The conservation of this biodiversity may appear to conflict with economic development and will require concerted efforts by ecologists, mining companies and stakeholders. This inventory represents a first step towards an integrated conservation plan for that fascinating flora.

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