

# Implication of plant-soil relationships for conservation and restoration of copper-cobalt ecosystems

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## Abstract

**Background** Chemical soil factors play an important role in generating and maintaining plant diversity. Naturally metal-enriched habitats support highly distinctive plant communities consisting of many rare and endemic species. Species of these plant communities possess remarkable physiological adaptations and are now being considered key elements in the implementation of green technologies aimed at phytoremediation of contaminated soils and post-mined soils. Several studies have emphasised that industrial mineral extraction results in serious damage to ecosystems and serious

threats to human health and leads to the extinction of metallophyte species. In the southeastern Democratic Republic of the Congo (DRC), mining activities represent a threat to the long-term persistence of communities located on metalliferous copper and cobalt outcrops and their associated endemic metallophytes, which are currently considered some of the most critically endangered plants in the world.

**Scope** Plant diversity conservation of metal-rich soils must assess soil-plant relationships at different scales (ecosystems, communities, and populations) to define in-situ and ex-situ conservation and restoration projects. This paper proposes a review of soil-plant relationships involved in plant diversity and endemism and their implications for biodiversity conservation and restoration.

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## Introduction

For decades, ecologists have attempted to understand the relationships between soil properties and plant diversity, as some soils are associated with high richness and endemism in plant species ([Whittaker et al. 2001](#); [Escudero et al. 2015](#)). A number of plant diversity hotspots are associated with nutrient-poor environments, notably in the Fynbos in South Africa, the Kwongan in southwestern Australia, and the Campos

Rupestres in Brazil (Cowling and Lombard 2002; Hopper and Gioia 2004; Lambers et al. 2010; Laliberté et al. 2013; Lambers 2014; Silveira et al. 2015). Regions with naturally metal-rich soils may also exhibit landscape and environmental heterogeneity, promoting high richness and endemism in plant species, such as New Caledonia (Pillon et al. 2010), Sabah (Malaysia) (van der Ent et al. 2015a), California (USA) (Brady et al. 2005), Cuba (Borhidi 1996), and southeastern Democratic Republic of Congo (DRC) (Küper et al. 2004; Faucon et al. 2010). The most widespread natural metalliferous outcrops across the world are ultramafic soils rich in nickel (Ni), chromium (Cr), iron (Fe), and magnesium (Mg) (Harrison and Rajakaruna 2011), but natural outcrops rich in Fe, manganese (Mn), copper (Cu), cobalt (Co), and other rare minerals also occur. These metalliferous outcrops support unique vegetation adapted to high metal concentrations (i.e., Ni, Cr, Fe, or Mg) and, in general, nutrient deficiency and cation imbalances. Vegetation occurring in metal-rich habitats may present an important proportion of endemic species (Rajakaruna 2004; Faucon et al. 2010; Anacker 2011). These endemics significantly contribute to the biodiversity of some regions of the world (Kruckeberg and Rabinowitz 1985; Jacobi et al. 2007; Anacker et al. 2014; van der Ent et al. 2015b). For example, in California, endemic species from ultramafic rock outcrops represent close to 12 % of the state endemic flora (Kruckeberg and Kruckeberg 1990; Safford et al. 2005); in New Caledonia, they correspond to almost 60 % of the island's indigenous flora (Jaffré 1992).

In addition, metallicolous flora represents a remarkable biological resource for eco-technological applications, especially phytoremediation of contaminated soils (Boisson et al. 2016; Shutcha et al. 2010, 2015; van der Ent et al. 2015c). Whiting et al. (2004) considered these species an “El Dorado” of genetic material, which could be used for decontamination or ecological restoration of metal-contaminated sites. Implications in eco-technologies are particularly enhanced with the valorisation of metals in biomass from hyper-accumulators in green chemistry (Zn, Ni, Platinum - Pt, Cu, Co, and Manganese - Mn) as catalysts in organic synthesis of molecules of interest (Losfeld et al. 2012; Escande et al. 2014; Grison 2014).

As metallicolous vegetation often occurs on economically valuable mineral deposits, many are threatened by quarrying and mining activities (Erskine et al. 2012; Faucon et al. 2011; Whiting et al. 2004). Moreover,

extraction processes may lead to the contamination of adjacent nonmetalliferous habitats by industrial wastes (smelts, waste water, etc.), which might impact local plant diversity. Establishment of conservation and/or restoration programmes for plant biodiversity of metal-rich habitats (in-situ and ex-situ conservation) requires the understanding of relationships between soil and plant diversity. Knowledge of ecological and biogeochemical processes governing ecosystems, communities, and populations is fundamental to defining and applying ecological restoration of disturbed habitats (Palmer et al. 1997).

In southeastern DRC, natural copper and cobalt outcrops (Cu-Co outcrops) host remarkable herbaceous communities that comprise the so-called “copper flora”. These outcrops form isolated and scattered hills in a landscape matrix of Miombo woodland (Duvigneaud and Denaeyer-De Smet 1963; Duvigneaud 1959; Fig. 1) (<http://copperflora.org/eflora>). The Cu-Co outcrops present a variety of habitats according to a variation of edaphic conditions, including the natural Cu-Co contamination level of the soil (Fig. 1). Mineralisation of the parent rocks and geological succession promotes the Cu and Co enrichment of the soils along the slope of the hills with concentrations of bioavailable Cu from 20 to 10,000 mg.kg<sup>-1</sup> and Co from 2 to 1000 mg.kg<sup>-1</sup> toward the top of the Cu hills. These plant communities host more than 600 species tolerant to high Co and Cu concentrations (Leteinturier 2002). Among those tolerant species, 57 have been identified as endemic from the Cu-Co outcrops (i.e., Cu-Co endemics). The region, due to its extremely metal-rich subsoil, is currently at the forefront of mining activity. In DRC, 70 % of metallophytes taxa (species or genera) are considered critically endangered (i.e., CR) and about 10 % would already have disappeared (Faucon et al. 2010, 2012a). In addition, southeastern DRC is one of the principal regions across the world presenting both environmental and public health issues associated with soil, air, and water contaminations resulting from an important Cu, Co, and uranium (U) extraction (Banza et al. 2009; Manda et al. 2010; Cheyns et al. 2014). There is an urgent need to develop conservation measures as well as restoration projects for the biodiversity of Cu and Co outcrops.

This paper reviews recent advances in our understanding of relationships between soil and plant diversity in metalliferous outcrops located in southeastern



**Fig. 1** **a b** and **c** General overview of copper and cobalt outcrops in Southeastern DRC (Democratic Republic of Congo), geographically isolated in the landscape matrix dominated by Miombo woodland on non-metalliferous soils; **d** chasmophytic vegetation

at the top of Cu-Co outcrops; **e** et **f** steppes on soils with high Cu-Co content; **g** steppic savannah on the slope and **h** steppic savannah on downslope with lower Cu-Co content

DRC and the implication of these contemporary researches in defining conservation and restoration

strategies for the Cu-Co ecosystems and their associated plant biodiversity.



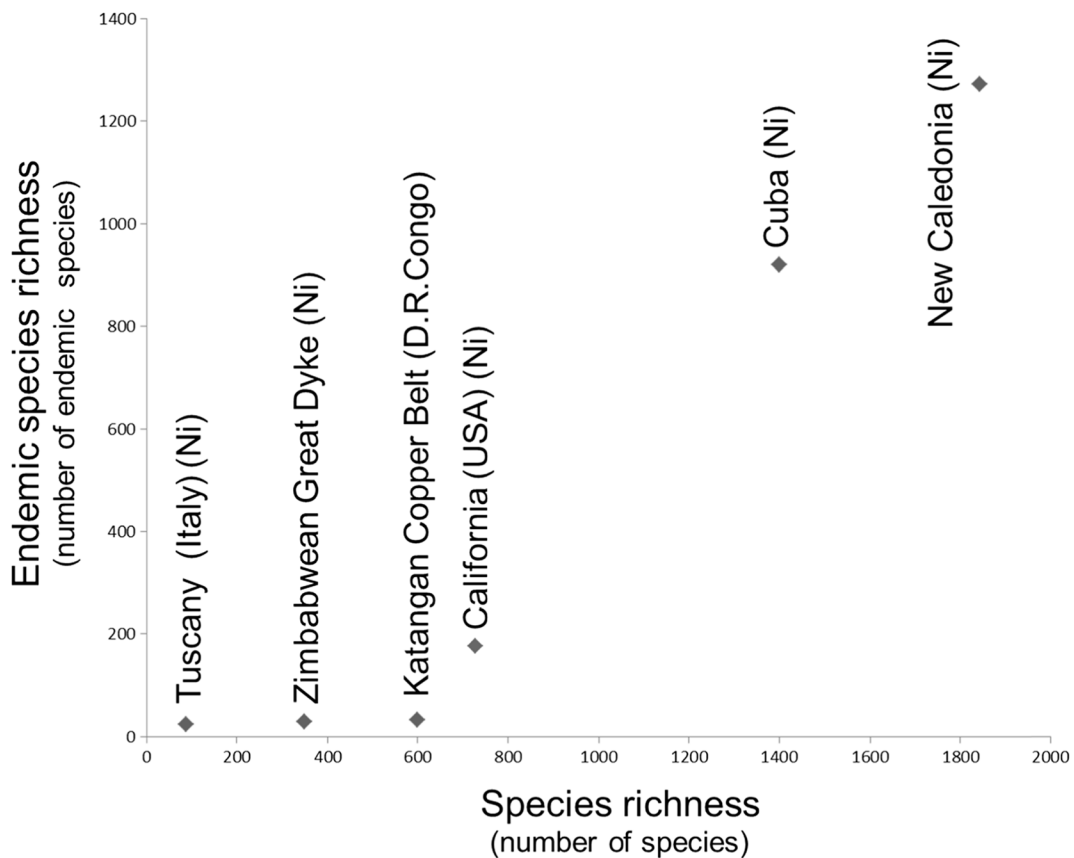
## Patterns of species richness and endemism on copper-cobalt outcrops

High Cu and Co concentrations in soil are phytotoxic and represent a strong selection pressure for plant species, which may induce ecological isolation and promote the speciation process (Duvigneaud and Denaeyer-De Smet 1963; Brooks and Malaisse 1990; Macnair and Gardner 1998). Among the approximate 600 plant species of flora of Cu-Co outcrops, 32 are strictly Cu-Co endemic (i.e., absolute metallophyte occurring exclusively on Cu-Co rich soils), and 23 are broad Cu-Co endemics (i.e., facultative metallophyte with more than 75 % of known populations occurring on Cu-Co rich soils) (Faucon et al. 2010). At outcrop scale, Cu and Co concentrations are a primary determinant of the richness of plant species. Outcrops with the highest Cu and Co concentrations in soil support the lowest total plant species richness (Duvigneaud and Denaeyer-De Smet 1963; Saad et al. 2012; Séleck et al. 2013). This pattern is in contrast to the richness of endemic metallophyte, which rises with the increase of Cu and Co concentration in the soil (Saad et al. 2012; Séleck et al. 2013). At the landscape scale, the spatial configuration of Cu-Co outcrops influences the richness of Cu-Co endemics of species. In a recent study of 34 Cu-Co outcrops varying in size (0.2 ha to 27.3 ha) and geographical isolation in a 30\*20 km landscape, Ilunga wa Ilunga (2014) demonstrated that Cu-Co endemic richness is positively correlated to the site surface, which might be associated with higher habitat diversity. Using species accumulation curves, it was demonstrated that the three largest outcrops encapsulate the total Cu-Co endemic richness (25 taxa) of the landscape, whereas at least 15 small Cu-Co outcrops are necessary to reach the same endemic richness.

How does endemic metallophyte richness in southeastern DRC compare with other metallicolous floras? The proportion of strict metallophyte endemic in the copper flora, estimated at 5 %, is obviously low when compared with ultramafic floras of California, Cuba, and New Zealand but is rather similar to ultramafic floras of Italy or Great Dyke (Fig. 2). Endemic richness and the endemism percentage depend on a combination of different variables (Harrison et al. 2006). The history of geographical isolation is important to explain endemism patterns. Cuba and New Caledonia are oceanic islands with a long history of geographical isolation resulting in a high global level of endemism (Fig. 2).

The age of exposure of metalliferous outcrops may also be an important factor to explain the proportion of endemics in a metallicolous flora (Harrison et al. 2004). Copper mineralisation in southeastern DRC dates from the late Cambrian period (about 620 myr, François 1973), but Cu-Co rich rocks have been exposed to plant colonisation for a much shorter period. Recent data indicate 2–3 myr as a likely age for Cu-Co outcrops (De Putter et al. 2010). This is similar to the age of exposure of California ultramafic outcrops (Harrison et al. 2004). Vegetation modification due to palaeoclimate variation might also be relevant to explain the endemism level in metallicolous floras. During the Holocene, tropical Africa experienced dramatic climate fluctuations, including a dry-cool period about 18,000 cal yr BP (Van Zinderen Bakker and Coetzee 1988; Vincens et al. 2005), with a deglacial period between 16,500 and 12,300 cal yr BP, including a retreat of montane elements at higher altitudes on the plateau under warmer conditions. This led to evolutionary divergences between populations isolated on the Cu-Co outcrops. These relatively recent divergences might explain the low percentage of endemic species observed in the copper flora. The close morphological resemblance between Cu-Co endemic plant species and more widespread counterparts, such as *Vigna dolomitica* and *V. reticulata* (Maxted et al. 2004), *Crotalaria peschiana* and *C. subcaespitosa* (Polhill 1982), *Acalypha cupricola*, *A. fuscescens*, and *A. dikuluwensis* (Levin et al. 2007), and *Silene burchellii* and *S. cobalticola* (Malaisse 1983), suggests that the speciation processes may be ongoing in the southeastern DRC region. This also supports the hypothesis that most of Cu-Co endemic species are neo-endemics (Malaisse 1983; Brooks and Malaisse 1985, 1990). This implies a recent divergence under intense ecological isolation (Macnair and Gardner 1998; Anacker and Strauss 2014). Another factor that may contribute to the low metallophyte endemism in southeastern DRC is the relatively low total surface of mineralised soils. Based on a typical site surface of a few tenths of a hectare, the total area of the Cu-Co outcrops may not exceed 100 km<sup>2</sup>, which is a small surface compared to the thousands of km<sup>2</sup> of ultramafic soil existing in California, Cuba, or New Caledonia (Harrison and Rajakaruna 2011). Eventually, ecological isolation and selective forces acting on populations occurring on Cu-Co rich soils may be overestimated. Unlike ultramafic soils, Cu-Co rich soils of southeastern DRC are relatively rich in nutrients (P, Ca, and Mg)





**Fig. 2** Relationship between total plant species richness and metallophyte endemic richness on natural metal rich soils in six metal world regions. Data are from Faucon et al. 2010

(Faucon et al. 2011; Séleck et al. 2013), and Cu soil toxicity might be mitigated by organic matter and other metals in oxidated forms (Lange et al. 2014; Pourret et al. 2015).

Even if metal-rich habitats are favourable environments for evolutionary divergence, the exceptionally high endemism occurring in such habitats remains intriguing (Kay et al. 2011). Intrinsic characteristics of metal-tolerant taxa may be responsible for the limitation of their ecological niche. One hypothesis for high endemism in metal-rich habitats might be a low ability of metallophyte to colonise non-metalliferous habitats due to constitutive needs in metals (Tadros 1957; Kay et al. 2011). For some Cu-Co endemic taxa, it has been demonstrated that biomass and fitness increase with Cu concentration in soil (Chipeng et al. 2009). Metal tolerance may also represent an adaptive cost responsible for a disadvantage of metallophyte in non-metalliferous soils (Macnair et al. 2000; Maestri et al. 2010) with a reduced competitive ability of metallophyte in non-

metalliferous habitats. Some studies support the hypothesis that the restricted distribution of metallophyte on metal-rich soils could be due to their low resistance to pathogens. Metal toxicity constitutes a strong selection pressure against pathogens and herbivores, limiting pathogen and herbivory pressures on metallophytes (Noret et al. 2005). As a result, metal tolerant taxa may also be characterised by a decrease in defence against herbivory and pathogens, which could limit their colonisation of non-metalliferous habitats (Faucon et al. 2012b; Kazakou et al. 2008). Very few data exist for Cu flora, but it has been shown that the Cu-Co endemic *Crepidorhopalon perennis* is able to grow on substrate without Cu only in axenic conditions (i.e., without soil biota) (Faucon et al. 2012b). However, this hypothesis is still controversial because some species of bacteria and fungi are perfectly adapted to metal-rich soils (Wakelin et al. 2014; Stefanowicz et al. 2008).

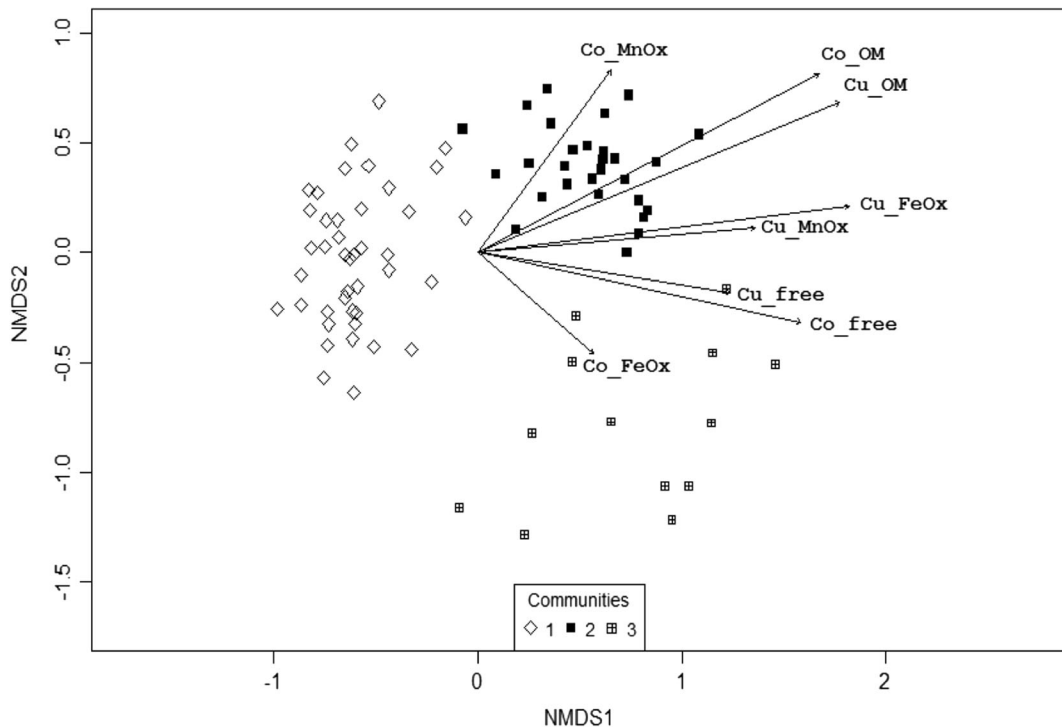
As a result of the complex interactions among physiological, ecological, and evolutionary factors, the

ecological niches of Cu-Co endemic from southeastern DRC vary widely (Faucon et al. 2011, 2012a). Congeneric species may present highly distinct edaphic niches. *Crepidiorhopalon perennis* (P.A. Duvigneaud) Eb. Fisch. (Linderniaceae), a Cu-Co endemic, occurs on soils richer in Cu compared to its pseudo-metallophyte congener *C. tenuis* (S. Moore) Eb. Fisch. (Faucon et al. 2011, 2012b). Boisson et al. (unpublished results) recently demonstrated that among eight Cu-Co endemic species present on the same Cu-Co outcrops, five have their optimum niches in the lowest concentrations of Cu (<300 mg Cu.kg<sup>-1</sup>) and Co (55 mg Co.kg<sup>-1</sup>) and only two have their optimum niches in the highest concentrations of Cu (>5000 mg Cu.kg<sup>-1</sup>). Species with their optimums in the higher Cu/Co concentrations also present the largest Cu/Co niche width. Ilunga wa Ilunga et al. (2013) found a similar pattern for non-endemic tolerant species on a Cu-Co outcrop in southeastern DRC. In addition, Ilunga wa Ilunga et al. (2013) demonstrated niche differentiation in relation to physical soil characteristics, namely rock cover and percentage of stones in the soil.

### Soil and plant communities' co-variation

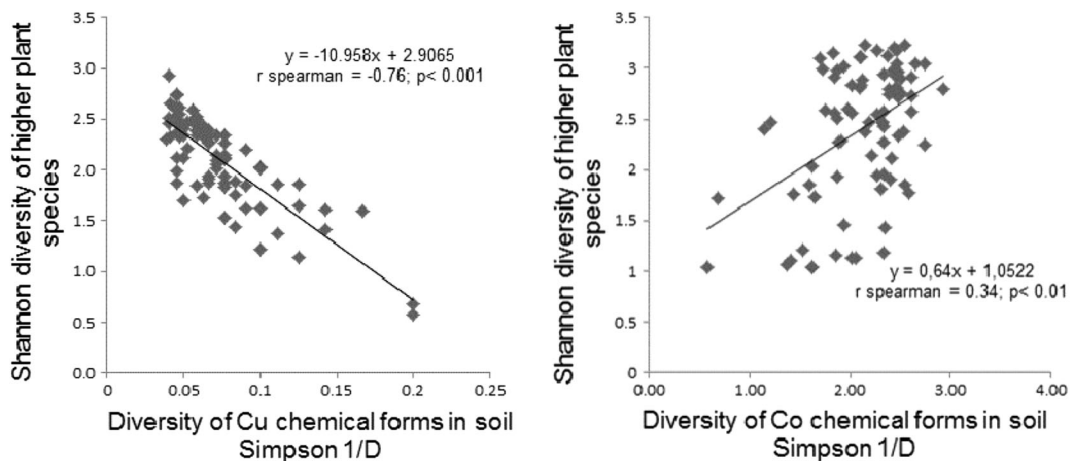
The physiognomy of vegetation varies on Cu-Co outcrops from the top to the bottom along a topographical gradient corresponding roughly to the Cu/Co gradient (Fig. 1). At the top, chasmophytic vegetation generally develops on poorly mineralised rocks (i.e., plant communities colonising the cracks and fissures of low mineralised rock with Cu concentrations of 250–900 mg kg<sup>-1</sup>). Steppe vegetation colonises the upper part of the outcrops with the highest Cu soil concentrations (ranging from 3500 to 35,000 mg kg<sup>-1</sup>). Finally, steppic savannah vegetation develops on the intermediate and foothill slopes and flat periodically flooded savannahs (dembos) at the bottom of the outcrops with Cu concentrations varying from 100 to 3500 mg kg<sup>-1</sup> (Duvigneaud and Denaeyer-De Smet 1963; Brooks and Malaisse 1985; Saad et al. 2012; Séleck et al. 2013) (Fig. 1). However, vegetation proved to be more complex than a simple succession of physiognomic plant formations along correlated Cu and Co gradients. More detailed studies revealed a mosaic of plant communities differing in species assemblages within and among Cu-Co outcrops (Saad et al. 2012; Séleck et al. 2013; Ilunga wa Ilunga et al. 2013).

Although (extractable) Cu and Co soil concentrations are the main factors correlated to variation in species composition among plant communities on Cu-Co outcrops, the mosaic of plant communities is also related to complex variations of other inter-correlated chemical factors. For example, in addition to differences in Cu-Co concentrations, steppic communities present higher values for pH, C, N, and extractable Ca and P (acetate-EDTA) and lower values for the C:N ratio and extractable Fe and K concentrations compared to steppic savannah communities. Besides the potential direct effect on species assemblages, soil factors, such as pH, C, Ca and Mn, can also contribute indirectly to floristic variation and heterogeneity of plant communities in Cu outcrops (Saad et al. 2012; Ilunga wa Ilunga et al. 2013; Séleck et al. 2013) because they can influence Cu and Co availability and toxicity (Lange et al. 2014; Pourret et al. 2015). Cobalt has a high affinity for manganese oxides (MnOx). A higher MnOx concentration in soil can decrease Co availability and toxicity (Collins and Kinsela 2011). In the same way, high concentrations of iron oxides and organic matter in soils can reduce Cu availability (Kabala and Singh 2001). Characterisation of metal speciation in soils also suggests a strong relationship between Cu and Co speciation in soils and structures of plant communities on a single Cu-Co outcrop (Fig. 3). A steppe community (Community 3 in Fig. 3) is associated with high concentrations of Cu and Co fractions that are considered available (i.e., Cu-Free, Cu-FeOx (Cu-iron oxides), Cu-MnOx, Co-Free, and Co-FeOx) (Lange et al. 2014). A second steppe community (Community 2 in Fig. 3) presents the highest concentrations of unavailable Cu and Co fractions (i.e., Cu-OM and Co-MnOx) and less Cu-Co-tolerant species. Variation of Cu and Co chemical forms in soils may create spatial heterogeneity of soil properties that influences a diversity of plant assemblages (Fig. 4). Diversity of Co chemical forms in soil influences positively plant species diversity. It may be hypothesised that the diversity of Co chemical forms in soil decreases Co availability and toxicity and promotes plant species diversity. However, diversity of Cu chemical forms in soil is negatively correlated to plant species diversity (Fig. 4). Given that most Cu chemical forms except Cu-OM can be available (i.e., Cu-Free, Cu-FeOx and Cu-MnOx) at pH of soils of Cu-Co outcrops (varying from 5 to 6) (Lange et al. 2014), diversity of Cu chemical forms would increase Cu availability and toxicity. However, these hypotheses should be tested in



**Fig. 3** Non-metric Multidimensional scaling (NMDS) ordination diagram of plots ( $n=83$ ) distributed in three different communities on a Cu-Co outcrop called Fungurume V. Data from Séleck et al. (2013). Fitted copper and cobalt fractions vectors are overlain by using the `envfit` command of `vegan` package (R statistical software, Oksanen et al. 2011). Copper and cobalt fractions in soils were modeled by speciation modeling (WHAM 6) from method of Pourret et al. (2015). MnOx: manganese oxides. FeOx: iron oxides. Community 1: Steppic savannah with *Cryptosepalum maraviense* (Caesalpiniaceae); *Loudetia simplex* (Poaceae) et

*Scleria bulbifera* (Cyperaceae) (Fig. 1 photo g and h). Community 2: Steppe with *Hyparrhenia diplandra* (Poaceae); *Schizachyrium brevifolium* (Poaceae); *Justicia elegantula* (Acanthaceae), *Michrochloa altera* (Poaceae); *Xerophyta equisetoides* (Velloziaceae) and *Bulbostylis cupricola* (Cyperaceae) (Fig. 1 photo f). Community 3: Steppe with *Pandiaka carsonii* (Amaranthaceae); *Ascolepis metallorum* (Cyperaceae); *Anisopappus davyi* (Asteraceae) (Fig. 1). The two dimensional solution of the NMDS had a final stress of 0.21 after seven iterations ( $R^2=0.79$ )



**Fig. 4** Relationship between 1/D Simpson diversity ( $D$ =Simpson's dominance index) of copper and cobalt chemical forms in soils with Shannon diversity of higher plant species ( $n=83$ ).

Copper and cobalt fractions in soils were modeled by speciation modeling (WHAM 6) from method of Pourret et al. (2015)



controlled conditions with a variation of metal-fractions to examine their effect on plant species diversity,

Nutrient content does not seem restrictive for the vegetation of Cu-Co outcrops; the amount of the essential macronutrients is higher on Cu-Co outcrops than on non-metalliferous soils in southeastern DRC (Saad et al. 2012; Séleck et al. 2013). This differs from ultramafic soils where deficiencies in N, P, K, and Ca have been suggested as a potential reason for limited plant productivity (O'Dell et al. 2006; Whittaker 1954). It can be thus inferred that selection pressure may be more strongly influenced by metal toxicity than by a high variation of nutrient content. However, the covariation of plant communities with nutrients, partly independent from metal availability (Séleck et al. 2013), suggests the need for a deeper exploration of the effect of N and P through the examination of the variation of the foliar N:P ratio and experimentation on P limitations along a Cu/Co gradient, where both the diversity and productivity of plant species should be measured (Aerts and Chapin 1999).

Variations of Cu and Co concentrations in soil also involve variations in trait responses of plant species. Delhaye et al. (2016) showed that the gradient of soil metal concentrations is associated with a pattern of trait substitution rather than high intraspecific trait variation. At the community-level, trait variation results in a shift in the abundances of various life forms. Xylopod species (i.e., with underground storage organs) are dominant in the lower part of the Cu-Co outcrops in communities occurring on deeper soils that are less rich in metal, whereas annual species are dominant in the upper part of the Cu-Co outcrop in communities located on more shallow soils with high metal concentrations (Séleck et al. 2013).

### **Implication of plant-soil relationships for conservation and restoration of plant biodiversity in Cu-Co outcrops in southeastern DRC**

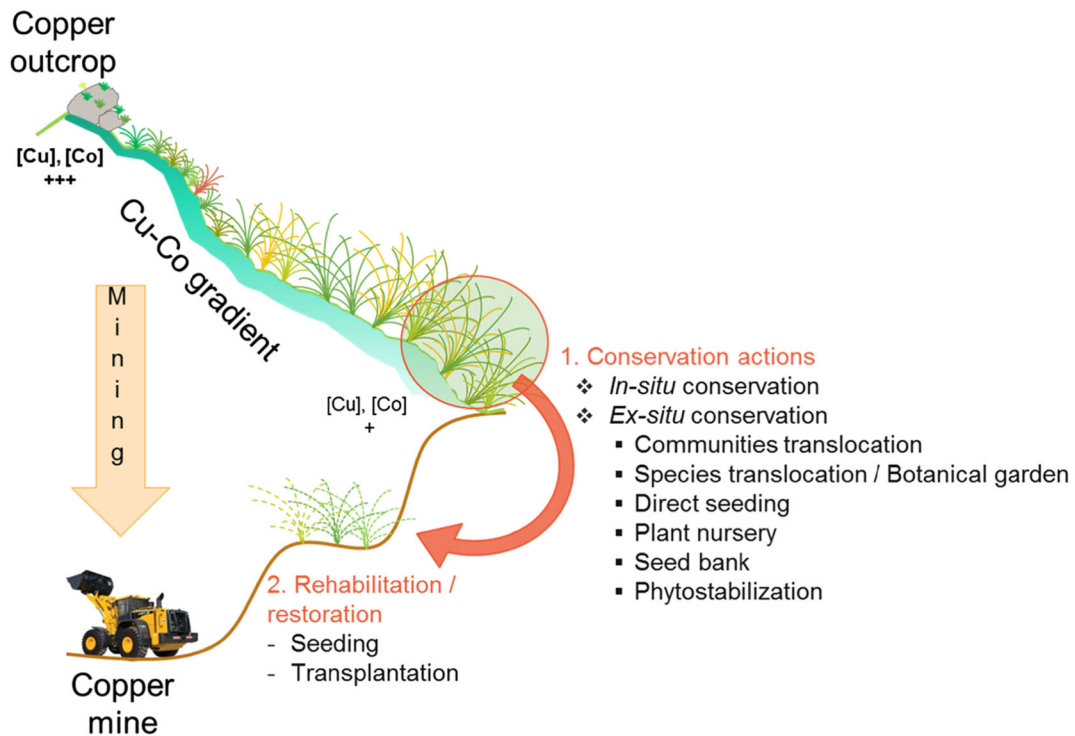
The first strategy from a biodiversity conservation point of view would include the preservation of a proportion of Co-Cu outcrops in protected areas. As demonstrated by endemism patterns at the landscape scale, the preservation of a limited number of Cu-Co outcrops occurring in southeastern DRC should allow the conservation of a set of populations of most Cu-Co endemic species. In contrast, the preservation of the diversity of plant

communities in untouched protected Cu-Co outcrops will be far more challenging. The high diversity of plant communities as well as the variability of plant assemblages among outcrops would need to preserve a large proportion of Cu-Co outcrops if ecosystem diversity must be addressed. This may turn out to be a limited and economically unrealistic option, considering the increasing demand for Cu and Co in the world and the high contribution of the Cu-Co market to the economy of the DRC.

A valuable alternative to preserving the extraordinary biological heritage of Cu-Co outcrops is to set up, prior to ecological restoration and rehabilitation of sites at mine closure, an ex-situ conservation strategy at the level of plant communities with topsoil and community translocation and at the level of individual species with translocation of individuals in restored habitats, conservation and multiplication in botanical gardens, and long term ex-situ seed banks for most characteristic species (<http://www.copperflora.org>: Conservation; Godefroid et al. 2013) (Fig. 5).

In this review, we have highlighted that extractable Cu-Co soil concentrations and other edaphic soil factors (i.e., pH, C, N, Ca, Mn, and Fe) are the main drivers structuring plant communities, and their variation is partly responsible for the heterogeneity of communities observed at the scale of the Cu-Co outcrops. Alteration and/or modifications of edaphic conditions of Cu-Co outcrops therefore have important consequences on vegetation composition and structure. Plant communities of Cu-Co outcrops are poorly or not resilient to strong anthropogenic disturbances, such as mineral extraction, made either by artisanal miners or mining companies (Ilunga wa Ilunga et al. 2015). The comparison, in terms of species composition and/or abundance of functional traits, between primary plant communities occurring on Cu-Co outcrops and secondary plant communities resulting from the re-colonisation of disturbed areas (i.e., altered areas after mineral extraction with potentially deposition of mining waste) did not show any functional resilience of the primary communities, even after 30 years of degradation by mining (Faucon et al. 2011; Ilunga wa Ilunga et al. 2015). Conservation or restoration of the soil factors is therefore necessary and crucial to conserve plant community on Cu-Co outcrops.

Plant community translocation projects through the transfer of topsoil and vegetation mats have been set up in southeastern DRC by Tenke Fungurume Mining, a



**Fig. 5** Global strategy of biodiversity of natural Cu and Co outcrops in a mining region

mining company (Fig. 5). The initial results of these translocations demonstrate that vegetation mat translocation is the most efficient method to preserve the biodiversity of Cu-Co outcrops compared to topsoil transfer (Le Stradic et al. 2016). In contrast to topsoil transfer, vegetation mat translocation allows transference of numerous species with fewer non-target species, probably due to a higher competition with the already established vegetation. For steppic savannahs, the seed bank is poor in species and seeds, and little emergence of target species (i.e., copper flora species) occurs in the topsoil, while ruderal species quickly colonise bare ground areas. Results are more encouraging for the steppe, given that high metal concentrations (i.e., Cu and Co) appear to limit the development of ruderal species, and a greater number of annual species provides a more rapid vegetation cover from the first year with some target species of copper flora (i.e., species present in the pristine Cu-Co communities), such as *Bulbostylis cupricola* Goetgh. or *Haumaniastrum robertii* (Robyns) P.A. Duvign. and Plancke. Steppic communities present shallow soils, favouring the transfer of the plant community without root damage. In contrast, vegetation mat translocation failed to transfer structuring xylopod species (i.e., dominant species) with important underground

systems, such as *Cryptosepalum maraviense* (Fabaceae). The absence of xylopods in translocated ecosystems may modify underground competition relationships within the community and promote the dominance of Poaceae species. While edaphic conditions are essential in order to restore Cu-Co communities properly, biotic filters and species interactions are also necessary to structure plant communities occurring on Cu-Co outcrops, and more research on this topic is necessary.

Ex-situ conservation of individual species also introduces great challenges. In this review, we have highlighted interspecific variations in realised ecological niches of Cu-Co endemics in relation to Cu and Co concentrations in soils but also other chemical and physical soil factors. This suggests that conservation strategies need to be species-specific and cannot be generalisable for all endemic metallophytes, particularly if the aim of the ex-situ conservation strategy is reintroducing and self-sustaining populations in restored habitats. In the short term, detailed studies are needed to characterise both the fundamental and realised niches of endemic metallophytes from Cu-Co outcrops (Schenk 2008). Characterisation of the fundamental niches of Cu-Co endemics (i.e., the physiological tolerance of a species in the absence of biotic interactions) will be

crucial to developing ex-situ conservation and multiplication programmes in botanical gardens before reintroduction in restored habitats.

Although species conservation priorities are generally based on rarity and species extinction threats (IUCN criteria), conservation strategies for Cu-Co metallophytes should also integrate the conservation of genetic diversity within the region. Some genetic variation of adaptive traits exists between populations of the same species. Genetic variation between populations of Cu tolerance and accumulation has been demonstrated in two pseudo-metallophytes, *Crepidiorhopalon tenuis* and *Haumaniastrum katangense* (Faucon et al. 2012b; Peng et al. 2012). This genetic variability of Cu tolerance and accumulation is an opportunity to select the most tolerant populations and define phytoremediation processes (phytoextraction or phytostabilisation).

## Conclusion

This review highlights advances in knowledge of plant diversity of natural Cu-Co outcrops at different scales or ecological levels (flora, ecosystems, plant species communities, and plant populations) in order to provide guidelines and identify knowledge gaps to define biodiversity conservation programmes. In mining regions where there is an obvious conflict of interest between economically important mining activities and conservation of plant biodiversity of natural metalliferous outcrops, there is an urgent need to define science-based strategies for biodiversity conservation, including in-situ and ex-situ approaches, ecosystem reconstruction, and post-mining restoration (Fig. 5). Ex-situ conservation prior to mining activities could be undertaken on available areas adjacent to mineralised outcrops with Cu-Co rich soils or Cu-Co enriched soils. Plant diversity, especially metallophytes, even in ex-situ conservation areas, is a genuine resource for phytoremediation of degraded post-mining areas. Future challenges are to conciliate biodiversity conservation and ecological engineering for phytoremediation of Cu-Co contaminated soils generated by mining activities. This goal will be reached only if a strong cooperation between scientists, field conservationists, and mining companies is set up. Considering the urgency of the situation, scientific studies should be a full part of conservation strategies. In turn, learning from true conservation experience needs to be designed now (research by design) and will be a

key method for increasing our scientific knowledge of this exceptional biological resource.

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