Small-scale diversity of plant communities and distribution of species niches on a copper rock outcrop in Upper Katanga, D.R.Congo

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Background and aims – In Katanga (D.R.Congo), outcrops of bedrocks naturally enriched in Cu and Co ("copper hills"), host unique plant communities. The spatial variation of vegetation has long been attributed almost exclusively to variation in Cu concentration in the soil, but this assumption has not been experimentally tested. We analysed the variation in plant communities and the niches of selected species in relation to edaphic factors within a copper hill.

Methods – Forty-eight 1 m^2 plots were sampled for plant community and soil mineral element composition, and classified with Unweighted Pair Group Method with Arithmetic mean (UPGMA) using the Bray-Curtis distance. Plant-edaphic relationships were examined using a Canonical Correspondence Analysis (CCA). Species niches were modelled with Generalized Additive Model (GAM). Mean edaphic factors between the soil of plant communities were compared with one-way Kruskal-Wallis non-parametric ANOVA.

Key results – The diversity of communities at the site scale was higher than observed in previous studies at a larger scale. Cu was the most discriminating edaphic factor of plant communities. However, detailed comparisons of mean edaphic factors among communities revealed individual combinations of edaphic parameters for each community, as well as differences in soil Cu content. High covariation appears to be an essential trait of the edaphic factor variation of Katangan Cu-rich soils. This makes it difficult to examine separately the effect of these factors on plant community structures. A bimodal pattern of niche distribution was found for Cu and pH. For physical parameters, niche optima were normally distributed.

Conclusions – Global variation in edaphic factors associated with variation in combinations of edaphic parameters generates a highly heterogeneous environment favourable to a high diversity of plant communities over limited areas. Conservation strategies or restoration actions to limit the impact of mining activities on Cu-enriched ecosystems should pay special attention to recreate heterogeneity, taking into account the covariation of edaphic factors.

Key words – conservation, copper, ecological niche, heavy metals, mining activities, plant community, vegetation.

INTRODUCTION

Identification of the factors that control the distribution and abundance of plant communities is a central problem in ecology, which can be addressed at all spatial scales, ranging from continental scales to patchy or highly restricted mi-

crohabitats (Keddy 2007). The problem of plant community variation is more often assessed over a large scale, encompassing obvious environmental gradients or patchy heterogeneity. However, it is clear that environments can also vary over very small spatial scales and this small-scale variation directly impacts on plant assemblages (Odum 1988, Vivian-

Smith 1997, Grace et al. 2011). Among the factors that are main contributors to the diversity and distribution of plant communities, edaphic conditions are of primary importance, whether they influence plant communities through resource availability, water stress or toxicity stress. From all the chemical edaphic factors that might influence plant assemblages, heavy metals have a long history of interest. Throughout the world, metal-rich soils host highly distinctive plant communities that result from deterministic species selection by environmental filters and random processes in insular habitats (Ernst 1974, Kruckeberg 1984, Bergmeier et al. 2009, Bes et al. 2010, Saad et al. 2012). Due to the severe selection pressure resulting from metal toxicity, they also offer outstanding examples of microevolution and speciation processes and very often host rare endemic taxa adapted to elevated concentrations of heavy metals (Antonovics et al. 1971, Brooks et al. 1982, Rajakaruna 2004, Faucon et al. 2010, Harrison & Rajakaruna 2011). Small scale variation in edaphic conditions in metalliferous sites have been demonstrated to affect physiological and evolutionary process (Malaisse et al. 1983, Bizoux et al. 2008, O'Dell & Rajakaruna 2011, Yost et al. 2012), species distribution (Rajakaruna 2004) and, ultimately, variation in plant assemblages (Ernst 1974, Bizoux et al. 2004, Tsiripidis et al. 2010).

Throughout the world, the flora of metalliferous soils is threatened by human activity and actions aimed at preserving metallophyte species are imperative (Whiting et al. 2004). Designing conservation and rehabilitation programmes, including restoration of habitats, is urgently needed, to limit the extinction risk of metallophyte plants and ecosystem loss (Whiting et al. 2004, ICMM 2006). Such a strategy relies on a sound understanding of the ecological niche of the target species and of factors that determine plant community composition at different spatial scales (Whiting et al. 2004, Chipeng et al. 2010, Faucon et al. 2012a).

Katanga (D.R.Congo) and adjacent areas of Zambia host one of the world's largest concentrations of Cu-Co deposits (Yoshida et al. 2004, Cailteux et al. 2005). Outcrops of bedrocks naturally enriched in Cu and Co, host highly original herbaceous plant communities, which sharply contrast with those of the surrounding forest (Duvigneaud 1958, Duvigneaud & Denaeyer-De Smet 1963). The Katangan metallicolous flora, known as the copper flora, hosts about 600 plant species tolerant to high concentrations of Cu-Co in soils (metallophytes) (http://copperflora.org/), 32 of which are strict endemics of metal-rich soil and 24 are broad endemics (Faucon et al. 2010). Katangan metallophytes represent an important biological resource to the D.R.Congo, as they might serve in the ecological restoration of heavy metal-polluted soils (Whiting et al. 2002, 2004, Faucon et al. 2010). Due to the revival of mining activities, most Katangan copper outcrops have been allotted to mining companies (Malaisse et al. 1999, Whiting et al. 2004) and will be irreversibly damaged in the coming decades. A number of endemics have already become extinct (Faucon et al. 2010, Faucon et al. 2012b).

Pioneering studies on these ecosystems, based on a classical phytosociological approach (Duvigneaud 1958, Duvigneaud & Denaeyer-De Smet 1963, Malaisse et al. 1994), revealed the existence of patterns of vegetation on copper

hills, with characteristic zonation along the slopes. Plant communities for each outcrop were organised along steep Cu gradients related to the outcrop topography (Duvigneaud & Denaeyer-De Smet 1963). However, plant communities described by physiognomic criteria did not provide a fine scale understanding of plant community diversity in relation to edaphic factors. Recent studies, based on modern sampling methods, support the idea that other soil factors, especially pH, Mn-oxides, Fe-oxides and organic matter should also be considered (Kabala & Singh 2001, Neaman et al. 2009, Faucon et al. 2011a). Interaction with metals other than Cu and Co might also limit their bioavailability and thus soil toxicity. Saad et al. (2012) suggested that nutrient status might also be of prime importance. To date, no detailed studies have focused on an assessment of the diversity of Cu plant communities in relation to edaphic factors at a small scale. Patchiness of metalliferous habitat might lead to high beta (inter-site) diversity for flora (Harrison & Inouye 2002, Harrison & Rajakaruna 2011), thus obscuring intra-site variation in large-scale studies. Examining the small-scale diversity of plant communities within single Cu sites is particularly important, to assess the effort that should be devoted to restoration strategies.

Apart from plant assemblages, single species belonging to similar plant communities are expected to react differently to the combination of environmental groupings. Understanding the individual niche of metallophyte species as well as the niche distribution along environmental gradients is essential for a fine-tuning of species conservation strategies in restored habitats (Bizoux et al. 2004, Chipeng et al. 2010, Faucon et al. 2011b). The ecological niches of only a few species growing on Cu outcrops have been characterised: *Ocimum centrali-africanum* (Howard-Williams 1970), *Haumaniastrum katangense* (Malaisse & Brooks 1982, Paton & Brooks 1996, Chipeng et al. 2010), *Mimulus cupriphilus*, *M. guttatus* (Macnair & Gardner 1998), *Crepidorhopalon perennis* and *C. tenuis* (Faucon et al. 2012b).

In this study, we address the degree to which small-scale continuous edaphic gradients can contribute to plant assemblage diversity and the consequences for restoration of metallophyte vegetation. The specific objectives of this study were to: (1) analyse the pattern of fine-scale plant community variation within a Cu site subject to a strong ecological gradient; (2) assess the distribution of ecological niches for a set of species representative of those communities for conservation and restoration purposes, and (3) compare our results with those of other studies performed on a larger scale, to infer implications for plant communities and species conservation at the small scale.

MATERIALS AND METHODS

Site description

Kinsevere outcrop is located at 11°36'S 27°58'E in the eastern part of the Katangan Copper Belt, 30 km north-north-east of Lubumbashi, D.R.Congo. The outcrop (surface approximately 9 ha, hill height around 25 m) is covered by swards on a plateau (1,263 m) with a gentle slope and flat area (contamination dembo) at the base of the outcrop, both character-

ized by steppic savannas. The copper hill is surrounded by miombo woodland with *Brachystegia* spp. Swards occur on reworked mine debris and consist of open vegetation mainly composed of annual species, long-lived short grasses and dicotyledonous species not exceeding 40 cm in height. Steppe savannas consist of dense vegetation on primary habitats dominated by long-lived tall grasses and dicotyledons with woody underground systems not exceeding 80 cm in height.

The climate is subtropical humid, CW6s according to the Köppen classification (Bultot 1950). There is one rainy season (November to March) and one dry season (May to September), with two transition months (October and April). Mean total annual rainfall is 1.273 mm of which 1.122 mm falls during the rainy season (Anvil Mining Compagny Katanga, unpubl. data). Mean annual temperature is 21°C. The temperature is the lowest at the beginning of the dry season (15–17°C). September and October are usually the warmest months with daily maxima of 31–33°C. The rainy season is characterised by the flowering of grasses and the dry season, by flowering of geophyte species stimulated by wildfires.

Soil sampling and vegetation cover estimation

Vegetation was sampled along two parallel transects (230 m in length) placed north-east to south-west along the main slopes. The transects were 25 m apart and encompassed the entire physiognomic variation of the outcrop's vegetation related to the topographic gradient. Forty eight permanent 1m^2 plots were located at 10 m interval along the transects.

To characterise plant communities, all plant species were recorded in each plot on four dates, corresponding to the phenological variation of Katangan vegetation: August 2008 (end of dry season), December 2008 (first part of wet season), February 2009 (mid wet season) and April 2009 (beginning of dry season). Species abundances were recorded using the Braun-Blanquet scale: +: < 1% cover, 1: 2–5% cover, 2: 6–25% cover, 3: 26–50% cover, 4: 51–75% cover and 5: 76–100% cover (Poore 1955). Nomenclature was based on the Flora Zambesiaca (Board of Trustees Kew Royal Botanic Gardens 1960–2010) and the Flore d'Afrique Centrale (Bamps 1973–1993). Authors of taxa and families to which they belong are given in the electronic appendix 1.

Plant collections were deposited at the herbaria of the Faculty of Agronomy (University of Lubumbashi) and the Biodiversity and Landscape Unit (Gembloux, Belgium). Composite soil samples (200 g) were collected in December 2008 in the upper soil layer (0–40 cm) of each plot. Each sample consisted of a bulk of five samples collected in the centre and the four corners of the 1 m^2 plot. Soil samples were air-dried and sieved to 2 mm and the percentage of stones (> 2 mm) was measured. The pH was measured in water or in 1N KCl with a glass electrode in a 2:5 soil:solution ratio and with 2h equilibration time. Total organic content was measured following the Springer-Klee method (Springer & Klee 1954), via hot oxidation with $K_2Cr_2O_7$ and titration of the excess oxidant with $(NH_4)_2Fe(SO_4)_26H_2O$. Total nitrogen was determined following the Kjeldahl method (Bremner & Mulvaney 1982). The bioavailability of Cu, Co, Zn, Fe, Mn, K, Mg, Ca and P were determined after an extraction by 1N CH$_3$COONH4EDTA (pH 4.65) for 30 min (ratio

soil:solution of 1:5) (Lakanen & Erviö 1971). The supernatant was filtered through a S&S 595 folded filter and analysed using a flame atomic absorption spectrometer (Varian 220). Phosphorus content was determined with a Shimadzu UV-1205 spectrophotometer (Shimadzu Corporation) at 430 nm after the development of blue colouration.

Identification of plant communities

Prior to statistical analysis, Braun-Blanquet coefficients were transformed into ordinal van der Maarel values: 1, 3, 5, 7, 8 and 9 (van der Maarel 2005). All seasonal relevés were compiled, selecting the highest abundance of each species in a plot. This method allows the phenological variation of flora in Katanga to be taken into account (Saad et al. 2012). Plant communities were identified through a hierarchical UPGMA classification using the Bray-Curtis distance (Dufrêne & Legendre 1997). The resulting hierarchical tree was analysed to define the main plant communities at 80% similarity. The 80% similarity criterion was selected, to allow comparison of results to those of recent studies (Saad et al. 2012). Indicator species for each plant community were identified with the IndVal method (Dufrêne & Legendre 1997). To examine the relationships between floristic data and the different edaphic variables, a Canonical Correspondence Analysis (CCA) was performed. Finally, one-way Kruskal-Wallis non-parametric ANOVA followed by Tukey's HSD test was performed to test differences between environmental variables among plant communities identified with the hierarchical classification (Oksanen 2010). Because edaphic parameters might covary along environmental gradients, we first explored the structure of edaphic factor variation at the study site via Principal Component Analysis (PCA).

Species ecological amplitude

The distribution of ecological niches along edaphic factors was explored for twelve species present in at least ten plots: *Andropogon schirensis*, *Bulbostylis pseudoperennis*, *Cryptosepalum maraviense*, *Digitaria nitens*, *Eragrostis racemosa*, *Gladiolus tshombeanus*, *Hibiscus rhodanthus*, *Loudetia simplex*, *Monocymbium ceresiiforme*, *Ocimum centrali-africanum*, *Scleria* sp. and *Tristachya bequaertii*. Generalised additive models (GAM; Hastie & Tibshirani 1990) – a non-parametric extension of generalised linear models (GLM) – with binomial likelihoods were used to model the probability of species abundance in relation to edaphic parameter values (Lepš & Šmilauer 1999) using CANOCO version 4.5 (ter Braak & Šmilauer 2002).

In a first step, each edaphic parameter pH water, pH KCl, Cu, Co, C, N, P, Cd, Zn, Fe, Mg, K, Pb, Mn, Ca, % rock cover, % stones in soil, slope) was separately tested against the twelve species. Only edaphic parameters for which at least half of the species had a significant GAM model (P < 0.01) were retained. To select the main factors potentially affecting species ecological niches at the studied site, we retained edaphic factors that best explained the abundance of the twelve selected species in a Canonical Correspondence Analysis (CCA). For each of the retained combinations, species-edaphic parameters, and the optimum and central border of the niche amplitude were estimated. The central

border is equivalent to the classical estimation of tolerance for the Gaussian response curve (Heegaard 2002, Heikkinen & Mäkipää 2010).

The fraction defining the central borders was computed following the formula: $c \times \exp(^{-2})$; with (c) as the maximum response (Heegaard 2002).

RESULTS

Edaphic factor variation

Variation among plant communities is the result of geochemical contamination primarily by Cu, possibly associated with Ca, Zn, Pb, Cd and to a lesser degree, the effect of organic matter. The first two axes of the PCA for eighteen edaphic variables explained 50% of the total variation (fig. 1). The variables that best correlated with PCA1 were Cu, pH KCl, N, C, Zn, Cd, Ca, Pb and P (positive correlation) and the variables best correlated with PCA2 were % rock cover,% stones in soil and Co (positive correlation) and K, Fe and Mg (negative correlation). On the second axis, without relation to the first axis, a greater % rock cover on the surface was associated with a greater % stones in soil and the poorest correlation was the habitat i.e. deficiencies in Mg, Fe and K (fig. 1). Altogether, the analysis suggests intercorrelation among numerous edaphic variables. Four main groups of parameters were identified: Cu-pH KCl-P, N-C-Zn-Cd, % rock cover-% stones in soil-Co, this latest opposed to Mg-Fe-K.
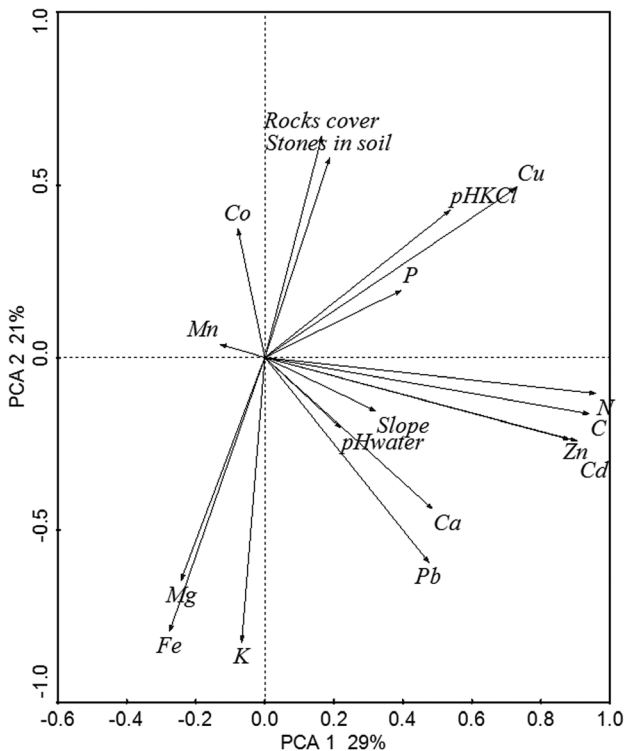

Figure 1 – Principal Component Analysis of 18 edaphic factors in 48, 1 m² plots on the Kinsevere copper outcrop. Arrows represent edaphic factors.

Plant communities

A total of 64 species were identified in the 48 plots. Five groups of plots were identified from the hierarchical classification at 80% similarity, and were interpreted as five different plant communities (fig. 2A & B). Each community was well characterized by a set of indicator species (fig. 2A & B).

Communities I and III corresponded to swards and steppe savanna, respectively, supplied with malachite gravel from the outcrop plateau. An indicator species for community I was *Haumaniastrum katangense*, an annual species. Community II corresponded to sward developing mainly on the plateau with a high proportion of malachite. Indicator species for community II were three short-stature perennial species with low rooting-depth systems: *Lapeirousia erythrantha*, *Ipomoea linosepala* subsp. *linosepala* and *Bulbostylis pseudoperennis*. Community III was characterised by *Commelina* sp., *Bulbostylis filamentosa* a short hemicryptophyte, and *Vernonia suprafastigiata*, a species developing a deep underground xylopode. Communities IV and V were typical steppe savannas located on different parts of the topographical gradient: the outcrop foot for community IV and dembo for community V. Community IV was characterised by *Tristachya bequaertii* and *Digitaria nitens*, two clonal gramineae, and *Cryptosepalum maraviense*, a soil-covering sub-shrub with well-developed underground xylopodes. Community V was also dominated by gramineous species; its indicator species were three sub-shrubs with well-developed underground xylopodes: *Eriosema englerianum*, *Hibiscus rhodanthus* and *Ocimum centrali-africanum* (fig. 2A & B).

Plant communities and edaphic factors

Five groups of relevés identified in the clustering analysis were distinguished well in the CCA analysis. The first two axes of the CCA explained 37% of the total variation. The first axis clearly opposed Communities I, II and III (positive values) to communities IV and V (negative values) and was positively correlated with trace metals and C-N content and negatively correlated with Mg, K and Fe.

Community II was also distinct from community I and III along axis 1 but the two latter communities were less distinguished. Axis 2 clearly separated communities IV and V, with negative coordinates for community IV being correlated mainly with slope, % of stones in soils and Fe.

There were differences in mean edaphic variables among the three communities for 12 of the 20 variables tested (table 1). Due to the number of tests and the intercorrelation of edaphic variables (table 1), associated probabilities should be taken with caution. However, careful examination of intercommunity differences highlights the complex nature of relationships among plant communities and edaphic parameters.

Cu was the best discriminating factor among communities ($F_{4,34} = 52.74$) and clearly distinguished communities I and III from community II with a high mean Cu content (1,131–12,874 mg/kg) and community IV from community V with a lower mean Cu soil content (111–289 mg/kg). The soil of community II not only exhibited the highest level of
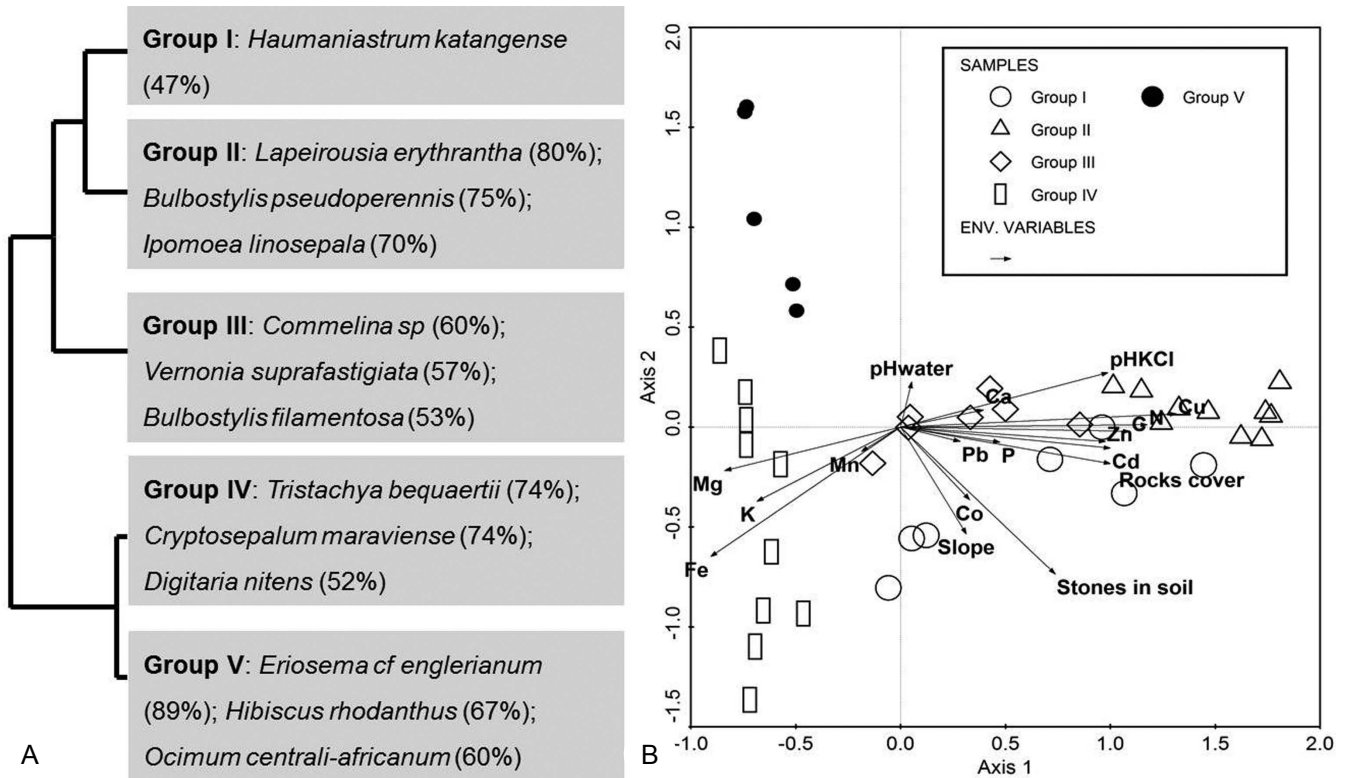
Figure 2 – Identification of plant communities, indicator species and relationships with edaphic parameters on the Kinsevere copper outcrop, Katanga, D.R.Congo. A, dendrogram generated from an UPGMA analysis performed on the Bray-Curtis distance similarity of species composition in 1 m² plots. Indicator species are shown with their IndVal value in brackets. B, canonical correspondence analysis (CCA) based on species composition and 18 environmental parameters in 48, 1 m² plots. The first two axes of the CCA explained 37% of the total variation.

Table 1 – Mean and standard errors of edaphic factors for the partitions in five communities identified at the Kinsevere copper outcrop.

*Significant differences in mean edaphic factors among groups after Bonferonni adjustment: $P < 0.003$. (Bonferonni adjustment: P value = 0.05/n variables); Superscript letters (a,b,c,d) indicate homogeneous groups (Tukey's HSD test, Kruskal Wallis non parametric ANOVA); n = number of samples per group. $F_{4,34}$ = Fischer significance test at 4 and 34 degree of freedom.

Environment variables	Group					$F_{4,34}$
	1 (n = 7)	2 (n = 10)	3 (n = 7)	4 (n = 10)	5 (n = 5)	
pHwater	5.2 (0.4)[a]	5.5 (0.3)[a]	5.4 (0.2)[a]	5.5 (0.2)[a]	5.4 (0.2)[a]	0.54
pHKCl	4.4 (0.3)[a]	4.8 (0.2)[b]	4.3 (0.2)[a]	4.3 (0.3)[a]	4.2 (0.1)[a]	6.77*
C (g/100)	1.7 (0.7)[a]	6.1 (1.5)[c]	4.3 (1.6)[b]	2.9 (0.5)[b]	2.1 (0.3)[a]	35.89*
N (g/100)	0.13 (0.05)[a]	0.44 (0.09)[c]	0.3 (0.12)[c]	0.19 (0.02)[b]	0.15 (0.02)[a]	29.66*
Cu (mg/kg)	1131 (1149)[c]	12874 (6099)[d]	1854 (1780)[c]	289 (84)[b]	111 (52)[a]	52.74*
Co (mg/kg)	6.6 (6.5)[a]	3.2 (4.1)[a]	3.4 (4.3)[a]	2.6 (2.2)[a]	2.5 (1.1)[a]	0.58
Zn (mg/kg	0.97 (0.7)[a]	4.89 (2.77)[b]	2.34 (1.93)[a,b]	1.58 (0.79)[a]	0.96 (0.23)[a]	9.14*
Cd (mg/kg)	0.03 (0.03)[a]	0.18 (0.09)[c]	0.11 (0.07)[b,c]	0.07 (0.02)[b]	0.03 (0.02)[a]	15.22*
Pb (mg/kg)	1.64 (0.89)[a]	2.77 (2.4)[a]	3.37 (2.54)[a]	2.29 (0.79)[a]	2.26 (0.23)[a]	0.76
Ca (mg/kg)	77 (72)[a]	176 (149)[a]	151 (108)[a]	124 (99)[a]	87 (63)[a]	1.35
Mg (mg/kg)	79 (31)[a,b]	57 (32)[a]	138 (48)[b,c]	196 (89)[c]	81 (36)[a,b]	12.93*
K (mg/kg)	76 (44)[a,b]	67 (46)[a]	110 (57)[a,b]	143 (48)[b]	101 (66)[a,b]	4.2
Mn (mg/kg)	49 (44)[a]	31 (39)[a]	48 (31)[a]	54 (32)[a]	24 (10)[a]	2.01
Fe (mg/kg)	65 (32)[a]	43 (21)[a]	115 (32)[b]	135 (34)[b]	60 (9)[a]	15.73*
P (mg/kg)	143 (237)[a]	213 (86)[b]	67 (43)[a]	83 (136)[a]	27 (5)[a]	8.44*
Slope (°)	11 (12)[a,b]	13 (7)[b]	13 (9)[b]	12 (5)[b]	0 (0)[a]	4.34*
Stones in soil (%)	52 (6)[c]	42 (11)[b,c]	30 (10)[a,b]	29 (10)[b]	17 (6)[a]	14.01*
Rocks cover (%)	77 (37)[c]	51 (32)[b,c]	13 (16)[a,b]	8 (7)[a]	0 (0)[a]	10.7*

Cu but was also distinguished from other communities by higher levels of C and P. The soil of community I, while exhibiting very similar levels of Cu to community III, was distinguished by lower levels of C and N.

Communities III and IV, while very different in Cu content, were both distinguishable from other communities by higher levels of Fe and, in part, Mg. The physical structure of the soil was also different among communities with soils of community IV and V, exhibiting a lower % stones in soil and lower % rock cover as compared to community I. Communities II and III showed intermediate mean values for these parameters.

Species ecological niches

For thirteen out of the eighteen edaphic variables, at least six species displayed a significant GAM model: % rock cover (n = 12); Cu (n = 10); pH KCl (n = 10); C (n = 9); N (n = 9); P (n = 9); Cd (n = 9); Zn (n = 8); Fe (n = 7); Mg (n = 7); K (n = 7); Pb (n = 7); % stones in soil (n = 6).

From these edaphic parameters, % rock cover, Cu, pH KCl and % stones in soil were the most prominent in ex-

plaining the variation in abundance of the twelve species in relation to edaphic factors based on a CCA analysis for these twelve species (not shown). Repartition of the niche optimum along the environmental gradients was different among the chemical and physical soil parameters (fig. 3). For Cu, ten species were situated with no niche optimum within the intermediate value, irrespective of the value of the gradient. The superimposition of ecological niches for Cu content was due to differences in niche amplitude among species with the highest optimum, also exhibiting the largest niche. A similar bimodal pattern was found for pH KCl. In contrast, niche optima were distributed normally along the gradient for physical parameters (% rock cover and % stones in soil), but a tendency to increase in niche amplitude with an increase in optimum values was also observed.

DISCUSSION

Pattern of fine scale plant community variation within a Cu site subjected to a strong ecological gradient

A small-scale gradient of environmental conditions is important to evolutionary processes, species coexistence and
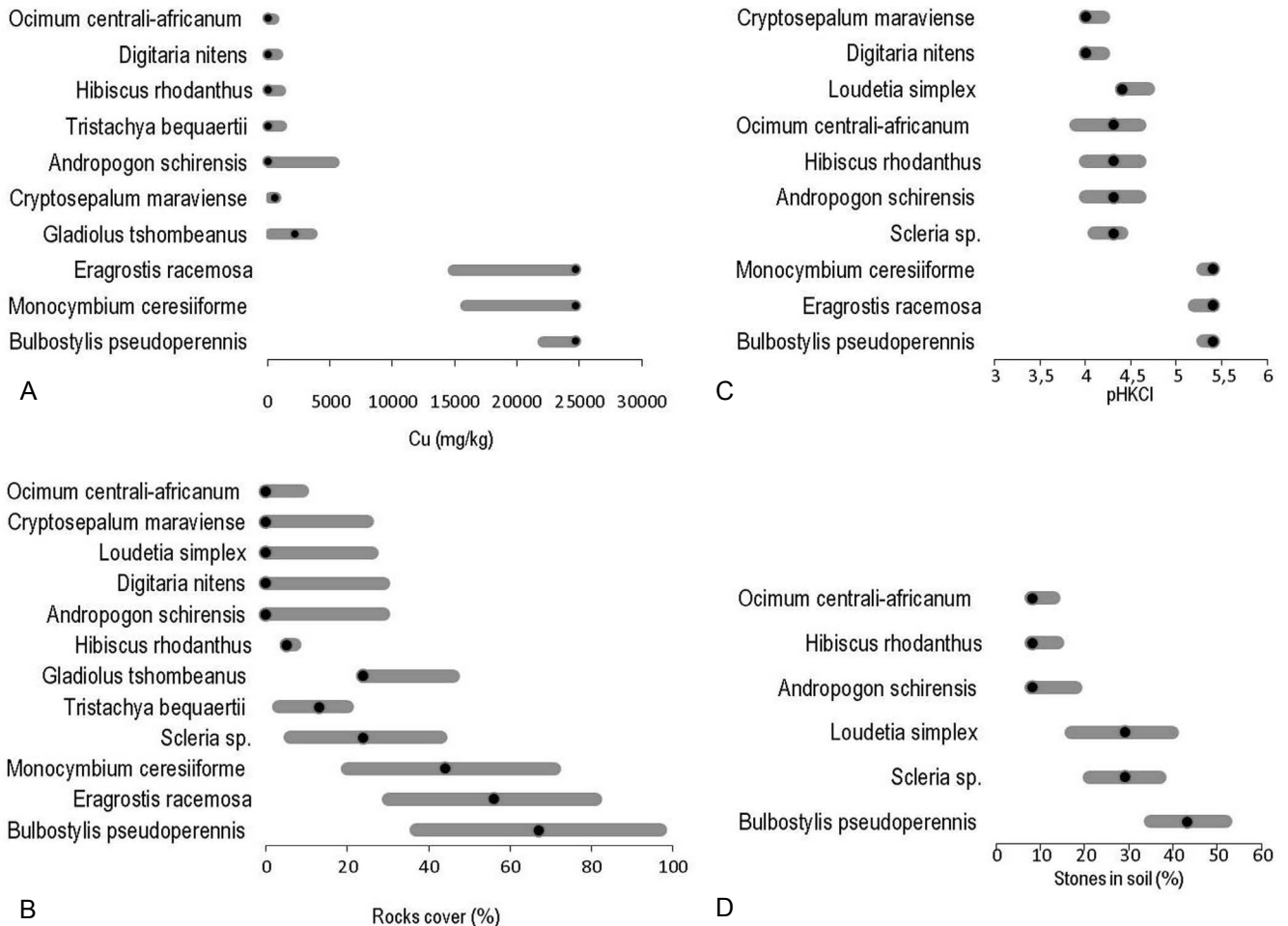

Figure 3 – Estimation of species ecological responses along environmental gradients with the optimum (black dot) and central borders (grey line). A, Cu; B, % rock cover; C, pH KCl; D, % stones in soil.

ultimately to the diversity of plant assemblages (Silvertown 2004). In this study, we found complex variation of edaphic conditions within a single metalliferous site. Such a complex pattern of edaphic variation is generated by a high covariation among edaphic factors. Small-scale edaphic variation within a single Cu site appeared as large as the variation demonstrated for combinations of Cu sites over a large spatial scale in both physical (stones in soil, rock cover) and chemical factors (Cu, Fe, Mg, P, K, N, C, and Zn) (Faucon et al. 2011b, 2012b, Saad et al. 2012). This variation in edaphic factors generates a highly heterogeneous environment, promoting niche diversity and therefore inducing a high diversity of plant assemblage over limited areas. The diversity of plant communities (N = 5) identified in our study site was higher than that (N = 3) identified by Saad et al. (2012) over six isolated Cu outcrops at a sub-regional scale based on the same criteria of analyzing plant-edaphic relationships.

This high local diversity of plant communities might be interpreted with respect to different combinations of edaphic conditions, in agreement with most recent studies on Cu vegetation (Faucon et al. 2011b, Saad et al. 2012). Obviously, due to its large variation, Cu concentration is the most discriminant edaphic factor among identified plant communities. However, not only variation in the concentration of Cu might be determinant for the structuration of plant diversity on Cu outcrops: analysis of covariation among floristic data and edaphic data (CCA) indicated a correlation of numerous edaphic factors with floristic variation.

Detailed comparisons of mean edaphic factors among communities also revealed individual combinations of edaphic parameters for each community apart from differences in soil Cu content. Nevertheless, correlations among edaphic factors should be taken with caution, given differences in soil properties due to horizon depth differences between habitats. Communities with a high level of soil Cu (I, II, III) also differed in other parameters including nutrients. Metallicolous communities associated with higher nutrient concentrations than other communities, differ from those on serpentine soils, where deficiency of N, P, K and Ca has been suggested as a potential reason for limited plant productivity (Kruckeberg 1984, O'Dell et al. 2006). Communities with a lower Cu contamination (IV, V) also differed from each other notably in Fe and Mg. Heavy metals are antagonistic to the uptake of other elements (Kazakou et al. 2008) and high values of Fe-oxides can limit Cu availability and thus its toxicity at low contamination levels (Kabala & Singh 2001). Furthermore, Fe is known to have antagonist effects on Cu uptake (Faucon et al. 2009). The large variation in physical properties of soil observed in our study should also play a role in filtering the assemblage of plants on Cu-rich soil. This might promote specific local conditions, such as reworked substrate typical of community I, where the therophytic pioneer species *Haumaniastrum katangense* dominates (Faucon et al. 2011b). Interestingly, Saad et al. (2012) found similar patterns of covariation in a multi-site study situated in another Katangan region (Tenke), with strong correlations within the same groups of edaphic factors: N-C and Fe-Mg-K. Covariation was shown by C and N, which is possibly explained by a high Cu content reducing mineralisation speed. The negative correlation between % stones in soil-rock cover and Mg-Fe-K might be explained by dilution of fine soil particles by quartz or by the presence of clayey rocks on the slope. High covariation appears to be an essential trait of edaphic factor variation of Katangan Cu-rich soils. This will make it difficult to examine separately the effect of these factors on plant community structures.

The plant communities identified in our study based on modern quantitative methods match closely the vegetation units identified via physiognomic criteria or traditional phytosociological approaches in pioneer studies (Duvigneaud 1958, Duvigneaud & Denaeyer-De Smet 1963). The first partition of the hierarchical clustering establishes the well-known distinction between low mineralized steppic savannas and highly contaminated swards. Individual communities might also be linked to previously described vegetation units: community I and III = swards with annual polycuprophytes on disturbed soil; community II = sward/steppe with polycuprophytes; community IV = steppic savanna on slope; community V = dembo steppic savanna.

Distribution of ecological species niches in heterogeneous environment

The concept of the ecological niche holds a central role in ecology as it has been widely used to understand species coexistence within communities and to predict species distribution along environmental gradients (Violle & Jiang 2009).

Wide variation in edaphic factors might also be expected to promote a diversity of ecological niches for individual species. Niche distribution along edaphic gradients has not been previously examined for species growing on Cu outcrops. Our results showed two different patterns for soil chemical and physical parameters. Niche optimum distribution was clearly bimodal for chemical factors, particularly for Cu. However, a high proportion of species with a niche optimum at the lowest Cu concentrations might partly be due to the fact that 67% of quadrats contained fewer than 1,000 ppm of soil Cu. In contrast, the distribution of the niche optimum was more regular along the gradient of physical parameters. Examination of niche amplitude also generates interesting hypotheses concerning the evolution of tolerance along edaphic gradients (Baack et al. 2006). For Cu, species with a niche optimum at higher concentrations displayed larger amplitudes and probably greater tolerance, than species with a niche optimum at lower concentrations. A similar pattern was observed for physical parameters (rock cover and stones in soil). These patterns should be interpreted with caution, due to the low number of species examined, but might suggest new hypotheses to be further tested in a larger context.

Fine-scaled ecological heterogeneity conditions probably play important roles in niche distribution. Some situations might cause divergent selection in the population and thus contribute to ecotypic differentiation (Antonovics et al. 1987, Bischoff et al. 2006).

In this study, the *Ocimum centrali-africanum* niche optimum, was limited only to soils with a lower Cu concentration compared to that in Howard-Williams (1970, 1971), where it was reported to vary in different soil types. This might be partly explained by constrained physical factors associated with the metal-rich soil of Katanga, namely % rock cover.

Ecological restoration, a challenge due to significant small-scale variation of plant assemblages

Our study demonstrated a high degree of small-scale diversity in plant communities (n = 5) along a Cu gradient in combination with several other edaphic factors. This is complementary to the lower diversity of plant communities found by Saad et al. (2012) at a regional scale. Hence, our results suggest the importance of further examination of Cu plant community diversity in a hierarchical spatial framework, if relevant conservation programmes have to be designed. Our results also indicate that maintaining the diversity of plant assemblages in post-mining rehabilitation programmes might be challenging, due to significant small-scale variation within those plant assemblages. With regard to restoration, actions to be promoted to limit the impact of mining activities on those ecosystems should pay special attention to the recreation of heterogeneous and specific conditions similar to those of plant communities (Pope et al. 2010, Lazarus et al. 2011). However, full restoration after re-establishing historic soil conditions will be achieved by avoiding changes in soil conditions, such as nutrient pollution, which alleviate edaphic stress (O'Dell & Classen 2011).

The largest amplitude of niches with an optimum in the most severe conditions (high Cu content; rocky substrates), suggests the possibility for those species to be maintained in alternative habitats, for example, in secondary habitats created by mining activities, given the intensity of natural habitat destruction. Such a situation was described by Faucon et al. (2011b) for a Cu metallophyte but needs to be tested further for other metallophytes in natural habitats and species with a phytoremediation potential.

SUPPLEMENTARY DATA

Supplementary data are available in pf format at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consists of a list of plant species sampled at the Kinsevere copper hill (Katanga, D.R.Congo)

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