



# Trace element hyperaccumulator plant traits: a call for trait data collection

Béatrice Gervais-Bergeron · Adrian L. D. Paul · Pierre-Luc Chagnon · Alan J. M. Baker · Antony van der Ent · Michel-Pierre Faucon · Celestino Quintela-Sabarís · Michel Labrecque

Received: 2 November 2022 / Accepted: 16 March 2023  
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2023

## Abstract

**Background and aims** Hyperaccumulator plants exhibit extreme ecophysiological characteristics, which make them suited for phytoremediation. Understanding their ecological strategies might help identify the species and functions to be favored in phytoremediation, restoration, and conservation projects for metalliferous sites.

**Methods** Here, we identified the hyperaccumulator species in the worldwide plant trait database TRY and cross-referenced these trait syndromes associated with the ability of plants to concentrate metals. This allows us to link trace element hyperaccumulation with broader plant ecological strategies.

**Results** Hyperaccumulator plant species tend to have smaller leaves and poorer competitive ability compared to non-hyperaccumulator plant species. Contrary to expectations, we found no indication of hyperaccumulator plants being more resource-conservative on the leaf economics spectrum. However, these data remain fragmentary as only 2.7% of

---

Responsible Editor: Enzo Lombi.

---

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11104-023-05996-7>.

---

B. Gervais-Bergeron (✉) · A. L. D. Paul · M. Labrecque  
Institut de recherche en biologie végétale, Université de Montréal, 4101 Sherbrooke East, Montréal, Québec H1X 2B2, Canada  
e-mail: [beatrice.gervais-bergeron@umontreal.ca](mailto:beatrice.gervais-bergeron@umontreal.ca)

P.-L. Chagnon  
Agriculture and Agrifood Canada, Saint-Jean-sur-Richelieu RDC, 430 boulevard Gouin, Saint-Jean-sur-Richelieu J3B 3E6, Canada

A. J. M. Baker · A. van der Ent  
Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, The University of Queensland, Brisbane, QLD 4072, Australia

A. J. M. Baker  
School of BioSciences, The University of Melbourne, Parkville, VIC 3010, Australia

A. J. M. Baker · A. van der Ent  
Laboratoire Sols et Environnement, Université de Lorraine – INRAE, UMR 1120, Nancy, France

A. van der Ent  
Laboratory of Genetics, Wageningen University and Research, Wageningen, The Netherlands

M.-P. Faucon  
UniLaSalle, AGHYLE (UP2018.C101), 19 rue Pierre Wagnet, 60026 Beauvais, France

C. Quintela-Sabarís  
Grupo de Ecoloxía Animal (GEA), Universidade de Vigo, E-36310 Vigo, Spain

hyperaccumulator plant species have their traits published in the TRY database.

**Conclusion** The recent development of trait-based models to construct plant communities providing optimal ecosystem services (e.g., phytoremediation, restoration) requires further research to identify predictable trait-service relationships. We thus call for an international collaborative sampling effort to measure traits in more hyperaccumulator plant species.

**Keywords** CSR strategies · Functional traits · Hyperaccumulation · Metallophytes · Plant functions · Synthesis analysis

## Introduction

Mining activities are major sources of pollution directly tied to human and environmental health issues worldwide. These activities severely threaten metalliferous ecosystems characterized by extreme environmental conditions (e.g., high metal concentrations, low resource availability), endangering some of the world's most biodiverse and endemic-rich communities (Myers et al. 2000; Baker et al. 2010; Ibanez et al. 2019). These ecosystems harbor a pool of species (i.e., metallophytes) with high ecological value and for use in contaminated land rehabilitation, phytomining, as well as metalliferous site restoration, and conservation (Whiting et al. 2004; Wójcik et al. 2017; Chaney et al. 2021; Quintela-Sabaris et al. 2020). Some metallophytes, called hyperaccumulators, are of particular interest because of their unique and extreme ability to accumulate trace elements (i.e., >100 times higher concentrations than most other plants) (van der Ent et al. 2013).

Although over 700 hyperaccumulator species have been identified so far (van der Ent et al. 2015b; Reeves et al. 2018), many questions concerning their ecological functions and potential applications remain unanswered (Lange et al. 2016), making it challenging to incorporate them into rehabilitation schemes (Reeves 2003; Kazakou et al. 2008; Kidd et al. 2015). Developing an approach to identify species and functions that can meet restoration or rehabilitation goals is, therefore, imperative. In this regard, a trait-based approach linking trace element accumulation strategies to plant morphology is a promising research avenue, given the wide array of plant traits that can be measured rapidly and the broad ecological processes

it can tackle (e.g., environmental filters, biogeochemical processes) (Laughlin 2014; Lange et al. 2016).

Metallophytes, including hyperaccumulators, often share common characteristics (morpho-physio-phenological traits), allowing for survival under the adverse conditions encountered on metalliferous sites (Violle et al. 2007; Baker et al. 2010). As a result, many generalizations have been made on their ecological traits and strategies, including (i) slow growth rates; (ii) investment in defense and secondary metabolites; (iii) multiple stress tolerances; (iv) extensive root system development; (v) high nutrient use efficiency (i.e., resource conservation strategy); (vi) investment in microbial nutritional symbioses (e.g., mycorrhizae or nitrogen-fixing bacteria); (vii) intolerance to shade and (viii) xeromorphic characteristics (Ernst 2006; Kazakou et al. 2008; Baker et al. 2010; Quintela-Sabaris et al. 2020; Paul et al. 2022). Moreover, because metalliferous soils are typically harsh environments with low vegetation cover and thus little competition over resources (Kazakou et al. 2008; Novakovskiy et al. 2021), metallophytes are generally categorized as stress-tolerators (*sensu* Grime 1988) with poor competitive ability and high capacity to conserve acquired resources (Wright et al. 2004; Ernst 2006; Baker et al. 2010; Maestri et al. 2010; Reich 2014; Lazzaro et al. 2021). These characteristics stand in contrast with fast resource-acquisitive species that invest in low-cost biomass to acquire resources rapidly but constantly invest in biomass replenishment, as more resources are lost to litter, predation, or parasitism (Reich 2014; Wright et al. 2004). As stress-tolerant species, hyperaccumulators are also expected to have smaller leaves and modest overall development (Pierce et al. 2017). Local studies have confirmed some of these trends with species, populations or ecotypes exposed to trace elements in soils (Kazakou et al. 2010; Adamidis et al. 2014; Lazzaro et al. 2021), as environmental factors may induce around 30% of intraspecific variability in traits (Albert et al. 2010). Nevertheless, it remains unknown whether these relationships hold at the global scale between hyperaccumulator and non-hyperaccumulator species. Although, it might be difficult to distinguish hyperaccumulator species from closely related non-hyperaccumulator species at such a large scale, traits-interspecific variability is generally high enough to distinguish broad tendencies. Moreover, since different metalliferous soils (e.g., ultramafic, calamine, seleniferous, Cu-Co rich soils) have distinct growth-limiting factors (e.g., fertility, climates) (Delhay et al. 2019; Garnica-Díaz et al. 2022), and since luxuriant

tropical forests and fast-growing ruderals can develop on metalliferous sites (Baker et al. 2010; Delhay et al. 2016; Galey et al. 2017), it remains unclear whether these environments select for stress tolerators or whether alternative strategies could allow functionally distinct species to establish in these environments (Samojedny et al. 2022). Focusing on a global scale means that resolution at the species or population levels would be limited, but it is an essential step to evaluate the generalizability and predictability of a trait-based approach.

To identify one or multiple hyperaccumulation strategies within a worldwide trait spectrum, we systematically evaluate linkages between leaf traits/ecological strategies and trace element hyperaccumulation by cross-referencing the plant trait database TRY (Kattge et al. 2019) and the global hyperaccumulator database (Reeves et al. 2018).

## Material and methods

Using the global plant trait database TRY (comprising data from >200,000 species), we gathered data on leaf area (LA - area of one leaf), specific leaf area (SLA - leaf surface area/dry mass ratio), and leaf dry matter content (LDMC - leaf dry mass/leaf fresh mass) (Kattge et al. 2019). These traits were selected to ensure broad species coverage (i.e., widely measured traits) while capturing essential components of plant strategies (Pierce et al. 2017). They are key traits on the economic spectrum strategies (Wright et al. 2004; Reich 2014) and help identify CSR strategies: Competitive (C), Stress-tolerant (S), and Ruderal (sensu Grime 1988). Moreover, traits related to nutrient acquisition, such as SLA and LDMC, might be associated with trace element accumulation (Lange et al. 2016). Species life forms were also obtained from the TRY database or the literature and subsequently categorized according to Pierce et al. (2013): trees, shrubs, forbs, graminoids, hydrophytes, and others (e.g., succulents, moss, and lichens). We further separated woody species (i.e., trees and shrubs) from non-woody species, as the presence of lignified tissues strongly covaries with the position of a plant along the resource acquisition-conservation spectrum (Pierce et al. 2013; Díaz et al. 2016). Potential hyperaccumulator species were first identified using the maximum concentrations of trace elements in leaves from the Global Hyperaccumulator Database (Reeves et al. 2018). The sources were validated to omit (i) non-peer-reviewed sources, (ii) data from hydroponic

and spiked soil experiments (van der Ent et al. 2015a), and (iii) records of foliar trace element concentrations below the hyperaccumulation thresholds (van der Ent et al. 2021). All species names were verified with the Taxonomic Names Resolution Service (TNRS), as recommended in TRY (Boyle et al. 2013; Kattge et al. 2019). All traits were averaged to species level, as is commonly done in global trait analysis (Díaz et al. 2016), and outliers were checked for possible data entry errors (Pérez-Harguindeguy et al. 2016). The final database contained 4523 species, of which 19 were hyperaccumulators (Table 1). The CSR strategies were calculated using the ‘Stratefy’ program based on LA, SLA, and LDMC species mean values (Pierce et al. 2017).

Generalized linear mixed models (GLM) with binomial distributions were used to link hyperaccumulation to leaf traits (i.e., LA, SLA, LDMC) and plant strategies (i.e., Grime’s C, S, and R scores). Model selection was based on AIC and pseudo- $R^2$  values and further validated with a likelihood ratio test. Traits were normalized before analysis: LA and SLA were log-transformed, and LDMC was logit-transformed. All analyses were performed in R (version 4.2.0) with the ‘stats’ package (R Core Team 2020) and the ‘AICcmodavg’ package (Mazerolle 2020).

## Results

The best predictors for hyperaccumulation were LA and LDMC, although the full model (i.e., LA + SLA + LDMC) performed equally well (no statistical difference between AIC). Both models explained only 5.7% of the variance (d.f. = 4522) and identified hyperaccumulators as having smaller leaves (LA,  $P < 0.05$ ) (Fig. 1a). However, this was not observed in hyperaccumulating woody taxa specifically ( $n = 4$ ) (Table S1), although this may simply result from low statistical power. Regarding the position of hyperaccumulators along the leaf economics spectrum a trade-offs between SLA and LDMC, we found no evidence for a conservative strategy with associated thicker leaves and high LDMC (Fig. 1a).

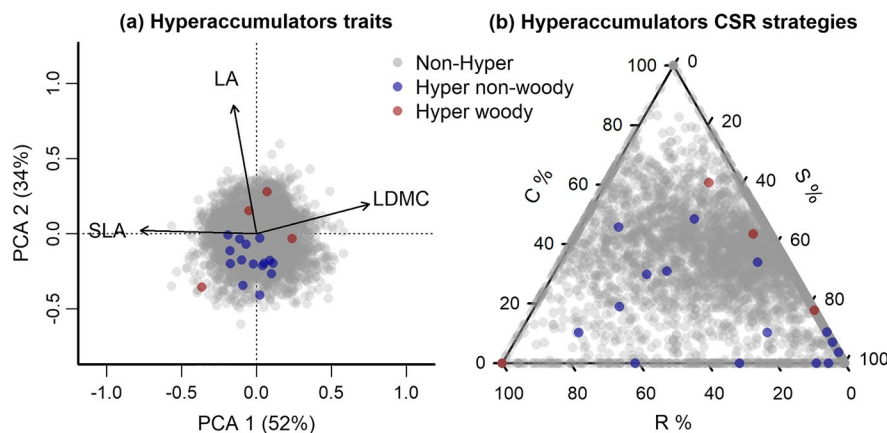
Hyperaccumulators also had significantly lower competitive ability (%C) ( $P < 0.05$ ), which was the only predictor retained through model selection for all hyperaccumulators and non-woody hyperaccumulators. Nevertheless, the model explained minimal variance (i.e., 3.1% for all hyperaccumulators and 3.4%

**Table 1** List of the 19 hyperaccumulators found on the global database TRY, their life forms, functional traits values, and hyperaccumulation elements

Family	Species	Life form	LA (mm <sup>2</sup> )	SLA (mm <sup>2</sup> g <sup>-1</sup> )	LDMC (mg g <sup>-1</sup> )	Trace element	Concentrations (mg kg <sup>-1</sup> )	Sources
Apocynaceae	<i>Carissa spinarum</i>	shrubs	339	9.46	0.47	Cu	700	(Rajakaruna and Bohm 2002)
Brassicaceae	<i>Arabidopsis halleri</i>	forbs	291	38.2	0.19	Zn	53,900	(Stein et al. 2017)
						Cd	3640	
Brassicaceae	<i>Odontarrhena tortuosa</i> (syn. <i>Alyssum tortuosum</i> )	forbs	21.7	15.3	0.33	Ni	1790	(Teptina and Paukov 2015)
Brassicaceae	<i>Nocca caerulea</i> (syn. <i>Thlaspi caerulea</i> )	forbs	114	30.3	0.15	Zn	53,500	(Reeves et al. 2001; Schwartz et al. 2006)
						Ni	16,200	
						Cd	2890	
Brassicaceae	<i>Nocca montana</i> (syn. <i>Thlaspi montanum</i> )	forbs	164	18.3	0.15	Ni	4300	(Boyd and Martens 1998)
Caryophyllaceae	<i>Minuartia verna</i>	forbs	3.66	22.5	0.29	Zn	3200	(Johnston and Proctor 1977)
Asteraceae	<i>Dieteria canescens</i> (syn. <i>Machaeranthera canescens</i> )	forbs	97.2	10.8	0.26	Zn	18,400	(Fellet et al. 2012)
						Tl	3630	(Fellet et al. 2012)
						Se	740	(Beath et al. 1941)
							1350	(Rosenfeld and Beath 1964)
Asteraceae	<i>Gutierrezia microcephala</i>	shrubs	19.6	69.5	0.10	Se	1290	(Beath et al. 1941)
Asteraceae	<i>Symphyotrichum ascendens</i>	forbs	96.4	10.5	0.21	Se	4460	(Pfister et al. 2013)
Asteraceae	<i>Symphyotrichum ericoides</i>	forbs	63.9	14.0	0.24	Se	3000	(El Mehdaoui et al. 2014)
Fabaceae	<i>Anthyllus vulneraria</i>	forbs	600	16.9	0.18	Zn	14,500	(Escarré et al. 2011)
Lamiaceae	<i>Stachys recta</i>	forbs	739	28.1	0.22	Ni	2600	(Lisanti 1952)
Fabaceae	<i>Astragalus canadensis</i> (syn. <i>Astragalus carolinianus</i> )	forbs	675	15.6	0.27	Se	1110	(Byers 1938)

Table 1 (Continued)

Family	Species	Life form	LA (mm <sup>2</sup> )	SLA (mm <sup>2</sup> g <sup>-1</sup> )	LDMC (mg g <sup>-1</sup> )	Trace element	Concentrations (mg kg <sup>-1</sup> )	Sources
Meliaceae	<i>Walsura pinnata</i>	trees	27.1	16.2	0.40	Ni	8000	(van der Ent et al. 2019)
Plantaginaceae	<i>Linaria alpina</i>	forbs	15.0	22.7	0.17	Ni	1990	(Vergnano Gambi and Gabrielli 1979)
Plumbaginaceae	<i>Armeria maritima</i>	forbs	95.1	15.0	0.19	Zn	5500	(Szarek-Lukaszewska et al. 2004)
						Cu	4230	(Farago et al. 1980)
Polygonaceae	<i>Rumex acetosa</i>	forbs	1510	29.1	0.15	Cu	1100	(Tang et al. 1999)
						Zn	11,000	(Johnston and Proctor 1977)
						Pb	5540	(Johnston and Proctor 1977)
Rubiaceae	<i>Psychotria grandis</i>	trees	9760	16.5	0.22	Ni	11,900	(Reeves 2003)
Saxifragaceae	<i>Saxifraga paniculata</i> (syn. <i>Saxifraga aizoon</i> )	forbs	83.5	8.75	0.24	Ba	2320	(Fehlauer et al. 2022)



**Fig. 1** Representation of hyperaccumulators' traits (a) and CSR strategies (b). Comparing all non-hyperaccumulators (gray circle,  $n=4503$ ), non-woody hyperaccumulators (blue circle,  $n=15$ ), and woody hyperaccumulators (red circle,

$n=4$ ) species available on TRY database. *Abbreviations:* leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), competitive (C), stress-tolerant (S), and ruderal (R)

for non-woody hyperaccumulators). Furthermore, no model could distinguish woody hyperaccumulator traits due to the small sample size ( $n=4$ ) and large dispersion. Overall, hyperaccumulators remained scattered across the CSR ternary plot and were poorly associated with any specific strategy (Fig. 1b). Finally, the CSR classification through leaf traits alone might be questionable for some species such as *Gutierrezia microcephala*, which is classified as a 100% R strategist, despite being usually described as a successional perennial species from desert habitats (Parker 1982).

## Discussion

Our preliminary results confirmed a weak trend for hyperaccumulator species to have smaller leaves, a trait often observed in flora from 'harsh' environments, such as metalliferous soils (Adamidis et al. 2014; Lazzaro et al. 2021; Sharma et al. 2021). Hyperaccumulator species were also relatively poorer competitors with more S and R strategies (e.g., shade-intolerant) (Ernst 2006; Baker et al. 2010). This is in line with the underrepresentation of competitive broadleaf species from hyperaccumulators. However, contrary to expectations (Kazakou et al. 2008; Adamidis et al. 2014), they were not consistently associated with the resource conservation end of the leaf economics spectrum. Nevertheless, it should be kept

in mind that all models performed poorly, which can be caused by a weak ecological signal at a global scale but also, potentially (and maybe primarily), by a lack of quality data on traits and strategies of hyperaccumulators.

The high variability in hyperaccumulator traits/strategies could also suggest that many alternative strategies have convergently evolved to promote trace element accumulation through various pathways. The accumulation strategy may change according to the metalliferous biogeochemical systems (i.e., ultramafic soil with Ni and Co or calamine soils with Zn, Pb, and Cd) or even the trace element accumulated. For example, co-occurring Ni and Co may be stored in different tissues and cell parts (i.e., vacuolar or exocellular sequestration) (Tappero et al. 2007; Rue et al. 2020; Paul et al. 2020b) or one specific trace element may accumulate in different tissues depending on the species and interactions with other trace elements (Broadhurst et al. 2009; Paul et al. 2020a). This may translate into alternative strategies of hyperaccumulation, relying on distinct plant traits/strategies. Detecting such alternative strategies at a global scale will require many more points than the 19 hyperaccumulator species from which we could gather reliable data in this study. Collecting more data on hyperaccumulator species is also necessary to address the non-independency between species and include some factors in further analysis (e.g., climate, phylogeny, habitat, life cycle, soil fertility)



(Broadley et al. 2001; Cappa and Pilon-Smits 2014; Joswig et al. 2022).

#### International trait data collection

Our preliminary study does not provide conclusive evidence for trait syndromes associated with trace element hyperaccumulation. We believe this may be primarily due to the lack of statistical power, given the poor representation of hyperaccumulators in the TRY database. A systematic review is currently underway to increase the hyperaccumulator species list. However, hyperaccumulator plant species remain underrepresented in trait databases, as they are often rare and localized species (Violle et al. 2015).

The lack of trait representation calls for a coordinated international effort to gather trait data on hyperaccumulators, particularly from locally endemic species. Non-hyperaccumulator metallophyte species should also be sampled to distinguish hyperaccumulation strategies and traits from those specifically involved in trace element tolerance. Future investigations could also focus on Ni hyperaccumulator species as they represent ~70% of identified hyperaccumulator species (Reeves et al. 2018) and would remove the noise associated with different metal accumulation.

Only a few leaves are necessary to inexpensively measure key leaf economic traits (LA, SLA, and LDMC). These leaves can be obtained from field specimens, gardens, or controlled experiments (if controls on metalliferous soil are available). Detailed protocols can be found in the *New handbook for standardized measurement of plant functional traits worldwide* (Pérez-Harguindeguy et al. 2016) and the TRY database (WEB cited protocols) (Kattge et al. 2019). Ideally, this approach should include more traits (i.e., plant height, seed mass, and stem-specific density) and nutrient leaf concentrations (P, K, N) (Lange et al. 2016). In addition, root traits (e.g., dry matter content, diameter, depth, P concentration) should also be considered to extend this approach, as they seem correlated with trace element accumulation and stress-tolerant strategies (Gervais-Bergeron et al. 2021; Lambers et al. 2015). To participate in this international sampling effort, we ask for measurements of metallophyte traits and their publication on the TRY database. To join this initiative or for further questions, contact the corresponding author.

#### Conclusion

This study is the first attempt to link plant traits to their ability to concentrate trace elements. Our results did not provide evidence for hyperaccumulators being necessarily characterized by a resource-conservative trait syndrome or a stress-tolerating strategy (according to Grime's framework and a classification based on leaf morphology alone). We believe that our inability to unravel trait syndromes among hyperaccumulators is rooted at least partly in a lack of reliable trait data. However, it may also well be that leaf morphology is a poor predictor of a plant's ability to concentrate trace elements at such a large scale (e.g., decoupled ecophysiological processes or limiting factors). Filling the gaps will be essential to guide applied land reclamation efforts and preserve metalliferous environments. We thus call for an international collaborative sampling effort to measure and share on TRY the traits of hyperaccumulator and metallophytes species.

**Acknowledgments** We acknowledge the essential contribution of researchers administering and contributing to the TRY database and the Global Hyperaccumulator Database. Your data sharing enables conducting of global analyses such as this.

**Author's contribution** Béatrice Gervais-Bergeron, Pierre-Luc Chagnon and Michel Labrecque conceived the ideas and designed methodology. Data were collected and analysed by Béatrice Gervais-Bergeron. The first draft of the manuscript was written by Béatrice Gervais-Bergeron, Adrian L.D. Paul, Pierre-Luc Chagnon and Michel Labrecque. All authors contributed critically to the drafts and gave final approval for publication.

**Funding** We acknowledge financial support from the Quebec Research Fund Nature and Technology (FRQNT No. 211259), the Natural Sciences and Engineering Council of Canada (NSERC), [funding reference number CGS D -569322-2022], the Federation of Canadian Municipalities (FCM), under the grant 'Use of phytoremediation to revitalize former industrial sites in eastern Montreal' and the Economic Development Division of the City of Montreal.

**Data availability** The data presented in this study are available on the repository of the University of Montreal, at <https://doi.org/10.5683/SP3/QKNQ08>.

#### Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

## References

- Adamidis GC, Kazakou E, Fyllas NM, Dimitrakopoulos PG (2014) Species adaptive strategies and leaf economic relationships across serpentine and non-serpentine habitats on Lesbos, Eastern Mediterranean. *PLoS One* 9:e96034. <https://doi.org/10.1371/journal.pone.0096034>
- Albert CH, Thuiller W, Yoccoz NG et al (2010) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits: intra- vs. interspecific variability in plant traits. *Funct Ecol* 24:1192–1201. <https://doi.org/10.1111/j.1365-2435.2010.01727.x>
- Baker AJM, Ernst WHO, van der Ent A et al (2010) Metallophytes: the unique biological resource, its ecology and conservation status in Europe, Central Africa and Latin America. In: Hallberg KB, Batty LC (eds) *Ecology of industrial pollution*. Cambridge University Press, Cambridge, pp 7–40
- Beath OA, Gilbert CS, Eppson HF (1941) The use of indicator plants in locating seleniferous areas in western United States. III. Further studies. *Am J Bot* 27:564–573. <https://doi.org/10.2307/2437092>
- Boyd R, Martens S (1998) Nickel hyperaccumulation by *Thlaspi montanum* var. *montanum* (Brassicaceae): a constitutive trait. *Am J Bot* 85:259–265. <https://doi.org/10.2307/2446314>
- Boyle B, Hopkins N, Lu Z et al (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinform* 14:16. <https://doi.org/10.1186/1471-2105-14-16>
- Broadhurst CL, Tappero RV, Mangel TK et al (2009) Interaction of nickel and manganese in accumulation and localization in leaves of the Ni hyperaccumulators *Alyssum murale* and *Alyssum corsicum*. *Plant Soil* 314:35–48. <https://doi.org/10.1007/s11104-008-9703-4>
- Broadley MR, Willey NJ, Wilkins JC et al (2001) Phylogenetic variation in heavy metal accumulation in angiosperms. *New Phytol* 152:9–27. <https://doi.org/10.1046/j.0028-646x.2001.00238.x>
- Byers HG, Miller JT, Williams KT (1938) Selenium occurrence in certain soils in the United States with a discussion of related topics: Third report. United States Department of Agriculture, Economic Research Service. <https://doi.org/10.22004/ag.econ.165916>
- Cappa JJ, Pilon-Smits EAH (2014) Evolutionary aspects of elemental hyperaccumulation. *Planta* 239:267–275. <https://doi.org/10.1007/s00425-013-1983-0>
- Chaney RL, Baker AJM, Morel JL (2021) The long road to developing agromining/phytomining. In: van der Ent A, Baker AJM, Echevarria G et al (eds) *Agromining: farming for metals: extracting unconventional resources using plants*. Springer International Publishing, Cham, pp 1–22
- Delhay G, Violle C, Séleck M et al (2016) Community variation in plant traits along copper and cobalt gradients. *J Veg Sci* 27:854–864. <https://doi.org/10.1111/jvs.12394>
- Delhay G, Hardy OJ, Séleck M et al (2019) Plant community assembly along a natural metal gradient in Central Africa: functional and phylogenetic approach. *J Veg Sci* 31:151–161. <https://doi.org/10.1111/jvs.12829>
- Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. *Nature* 529:167–171. <https://doi.org/10.1038/nature16489>
- El Mehdawi AF, Reynolds RJB, Prins CN et al (2014) Analysis of selenium accumulation, speciation and tolerance of potential selenium hyperaccumulator *Symphyotrichum ericoides*. *Physiol Plant* 152:70–83. <https://doi.org/10.1111/ppl.12149>
- Ernst WHO (2006) Evolution of metal tolerance in higher plants. *For Snow Landsc Res* 80:251–274
- Escarré J, Lefèvre C, Raboyeau S et al (2011) Heavy metal concentration survey in soils and plants of the Les Malines mining district (Southern France): implications for soil restoration. *Water Air Soil Pollut* 216:485–504. <https://doi.org/10.1007/s11270-010-0547-1>
- Farago ME, Mullen WA, Cole MM, Smith RF (1980) A study of *Armeria maritima* (Mill) willdenow growing in a copper-impregnated bog. *Environ Pollut Ser A Ecol Biol* 21:225–244. [https://doi.org/10.1016/0143-1471\(80\)90167-1](https://doi.org/10.1016/0143-1471(80)90167-1)
- Fehlauer T, Collin B, Angeletti B et al (2022) Uptake patterns of critical metals in alpine plant species growing in an unimpacted natural site. *Chemosphere* 287:132315. <https://doi.org/10.1016/j.chemosphere.2021.132315>
- Fellet G, Pošćić F, Casolo V, Marchiol L (2012) Metallophytes and thallium hyperaccumulation at the former Raibl lead/zinc mining site (Julian Alps, Italy). *Plant Biosyst* 146:1023–1036. <https://doi.org/10.1080/11263504.2012.703250>
- Galey ML, van der Ent A, Iqbal MCM, Rajakaruna N (2017) Ultramafic geoecology of south and Southeast Asia. *Bot Stud* 58:18. <https://doi.org/10.1186/s40529-017-0167-9>
- Garnica-Díaz C, Berazaín Iturralde R, Cabrera B et al (2022) Global plant ecology of tropical ultramafic ecosystems. *Bot Rev*. <https://doi.org/10.1007/s12229-022-09278-2>
- Gervais-Bergeron B, Chagnon P-L, Labrecque M (2021) Willow aboveground and belowground traits can predict phytoremediation services. *Plants* 10:1824. <https://doi.org/10.3390/plants10091824>
- Grime JP (1988) The C-S-R model of primary plant strategies — origins, implications and tests. In: Gottlieb LD, Jain SK (eds) *Plant evolutionary biology*. Springer, Netherlands, Dordrecht, pp 371–393
- Ibanez T, Birnbaum P, Gâteblé G et al (2019) Twenty years after Jaffré et al. (1998), is the system of protected areas now adequate in New Caledonia? *Biodivers Conserv* 28:245–254. <https://doi.org/10.1007/s10531-018-1659-y>
- Johnston WR, Proctor J (1977) A comparative study of metal levels in plants from two contrasting lead-mine sites. *Plant Soil* 46:251–257. <https://doi.org/10.1007/BF00693131>
- Joswig JS, Wirth C, Schuman MC et al (2022) Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nat Ecol Evol* 6:36–50. <https://doi.org/10.1038/s41559-021-01616-8>
- Kattge J, Bönsch G, Díaz S et al (2019) TRY plant trait database — enhanced coverage and open access. *Glob Chang Biol* 26:119–188. <https://doi.org/10.1111/gcb.14904>
- Kazakou E, Dimitrakopoulos P, Baker AJM et al (2008) Hypotheses, mechanisms and trade-offs of tolerance and adaptation to serpentine soils: from species to ecosystem level. *Biol Rev* 83:495–508. <https://doi.org/10.1111/j.1469-185X.2008.00051.x>



- Kazakou E, Adamidis G, Baker AJM et al (2010) Species adaptation in serpentine soils in Lesbos Island (Greece): metal hyperaccumulation and tolerance. *Plant Soil* 332:369–385. <https://doi.org/10.1007/s11104-010-0302-9>
- Kidd P, Mench M, Álvarez-López V et al (2015) Agronomic practices for improving gentle remediation of trace element-contaminated soils. *Int J Phytoremed* 17:1005–1037. <https://doi.org/10.1080/15226514.2014.1003788>
- Lambers H, Hayes PE, Laliberté E et al (2015) Leaf manganese accumulation and phosphorus-acquisition efficiency. *Trends Plant Sci* 20:83–90. <https://doi.org/10.1016/j.tplan.2014.10.007>
- Lange B, van der Ent A, Baker AJM et al (2016) Copper and cobalt accumulation in plants: a critical assessment of the current state of knowledge. *New Phytol* 213:537–551. <https://doi.org/10.1111/nph.14175>
- Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol Lett* 17:771–784. <https://doi.org/10.1111/ele.12288>
- Lazzaro L, Colzi I, Ciampi D et al (2021) Intraspecific trait variability and genetic diversity in the adaptive strategies of serpentine and non-serpentine populations of *Silene paradoxa* L. *Plant Soil* 460:105–121. <https://doi.org/10.1007/s11104-020-04780-1>
- Lisanti EL (1952) Contributo allo studio delle morfosi che si riscontrano sui serpentinei (possibilità di chemiomorfosi). *G Bot Ital* 59:349–360. <https://doi.org/10.1080/11263505209431540>
- Maestri E, Marmioli M, Visioli G, Marmioli N (2010) Metal tolerance and hyperaccumulation: costs and trade-offs between traits and environment. *Environ Exp Bot* 68:1–13. <https://doi.org/10.1016/j.envexpbot.2009.10.011>
- Mazerolle MJ (2020) AICcmodavg: model selection and multi-model inference based on (Q)AIC(c)
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Novakovskiy AB, Kanev VA, Markarova MY (2021) Long-term dynamics of plant communities after biological remediation of oil-contaminated soils in far north. *Sci Rep* 11:4888. <https://doi.org/10.1038/s41598-021-84226-5>
- Parker MA (1982) Association with mature plants protects seedlings from predation in an arid grassland shrub, *Gutierrezia microcephala*. *Oecologia* 53:276–280. <https://doi.org/10.1007/BF00545677>
- Paul ALD, Harris HH, Erskine PD et al (2020a) Synchrotron  $\mu$ XRF imaging of live seedlings of *Berkheya coddii* and *Odontarrhena muralis* during germination and seedling growth. *Plant Soil* 453:487–501. <https://doi.org/10.1007/s11104-020-04591-4>
- Paul ALD, Nkrumah PN, Echevarria G et al (2020b) Cobalt hyperaccumulation in *Rinorea* cf. *bengalensis* (Violaceae) from Sabah: accumulation potential and tissue and cellular-level distribution of cobalt. *Plant Soil* 455:289–303. <https://doi.org/10.1007/s11104-020-04629-7>
- Paul ALD, Isnard S, Brearley FQ et al (2022) Stocks and biogeochemical cycling of soil-derived nutrients in an ultramafic rain forest in New Caledonia. *For Ecol Manag* 509:120049. <https://doi.org/10.1016/j.foreco.2022.120049>
- Pérez-Harguindeguy N, Díaz S, Garnier E et al (2016) Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* 64:715. [https://doi.org/10.1071/BT12225\\_CO](https://doi.org/10.1071/BT12225_CO)
- Pfister JA, Davis TZ, Hall JO (2013) Effect of selenium concentration on feed preferences by cattle and sheep. *J Anim Sci* 91:5970–5980. <https://doi.org/10.2527/jas.2013-6595>
- Pierce S, Brusa G, Vagge I, Cerabolini BEL (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Funct Ecol* 27:1002–1010. <https://doi.org/10.1111/1365-2435.12095>
- Pierce S, Negreiros D, Cerabolini BEL et al (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Funct Ecol* 31:444–457. <https://doi.org/10.1111/1365-2435.12722>
- Quintela-Sabaris C, Faucon M-P, Repin R et al (2020) Plant functional traits on tropical ultramafic habitats affected by fire and mining: insights for reclamation. *Diversity* 12:248. <https://doi.org/10.3390/d12060248>
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rajakaruna N, Bohm BA (2002) Serpentine and its vegetation: a preliminary study from Sri Lanka. *J App Bot* 76:20–28
- Reeves RD (2003) Tropical hyperaccumulators of metals and their potential for phytoextraction. *Plant Soil* 249:57–65. <https://doi.org/10.1023/A:1022572517197>
- Reeves RD, Schwartz C, Morel JL, Edmondson J (2001) Distribution and metal-accumulating behavior of *Thlaspi caerulescens* and associated metallophytes in France. *Int J Phytoremediation* 3:145–172. <https://doi.org/10.1080/15226510108500054>
- Reeves RD, Baker AJM, Jaffré T et al (2018) A global database for plants that hyperaccumulate metal and metalloid trace elements. *New Phytol* 218:407–411. <https://doi.org/10.1111/nph.14907>
- Reich PB (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J Ecol* 102:275–301. <https://doi.org/10.1111/1365-2745.12211>
- Rosenfeld I, Beath OA (1964) Selenium: geobotany, biochemistry, toxicity, and nutrition. Academic Press, New York
- Rue M, Paul ALD, Echevarria G et al (2020) Uptake, translocation and accumulation of nickel and cobalt in *Berkheya coddii*, a ‘metal crop’ from South Africa. *Metallomics* 12:1278–1289. <https://doi.org/10.1039/d0mt00099j>
- Samojedny TJ, Garnica-Díaz C, Grossenbacher DL et al (2022) Specific leaf area is lower on ultramafic than on neighbouring non-ultramafic soils. *Plant Ecol Divers* 15:243–252. <https://doi.org/10.1080/17550874.2022.2160673>
- Schwartz C, Sirguy C, Peronny S et al (2006) Testing of outstanding individuals of *Thlaspi caerulescens* for cadmium phytoextraction. *Int J Phytoremed* 8:339–357. <https://doi.org/10.1080/15226510600992964>
- Sharma P, Ahmad M, Rathee S et al (2021) Bridging the gap: linking morpho-functional traits’ plasticity with hyperaccumulation. *Environ Monit Assess* 193:762. <https://doi.org/10.1007/s10661-021-09504-1>
- Stein RJ, Höreth S, de Melo JRF et al (2017) Relationships between soil and leaf mineral composition are element-specific, environment-dependent and geographically structured in the emerging model *Arabidopsis halleri*. *New Phytol* 213:1274–1286. <https://doi.org/10.1111/nph.14219>

- Szarek-Łukaszewska G, Słysz A, Wierzbicka M (2004) Response of *Armeria maritima* (mill.) Willd. to Cd, Zn and Pb. *Acta Biol Crac Ser Bot* 46:19–24
- Tang S, Wilke B-M, Huang C (1999) The uptake of copper by plants dominantly growing on copper mining spoils along the Yangtze River, the People's Republic of China. *Plant Soil* 209:225–232. <https://doi.org/10.1023/A:1004599715411>
- Tappero R, Peltier E, Gräfe M et al (2007) Hyperaccumulator *Alyssum murale* relies on a different metal storage mechanism for cobalt than for nickel. *New Phytol* 175:641–654. <https://doi.org/10.1111/j.1469-8137.2007.02134.x>
- Teptina AY, Paukov AG (2015) Nickel accumulation by species of *Alyssum* and *Noccaea* (Brassicaceae) from ultramafic soils in the Urals, Russia. *Aust J Bot* 63:78–84
- van der Ent A, Baker AJM, Reeves RD et al (2013) Hyperaccumulators of metal and metalloid trace elements: facts and fiction. *Plant Soil* 362:319–334. <https://doi.org/10.1007/s11104-012-1287-3>
- van der Ent A, Baker AJM, Reeves RD et al (2015a) Commentary: toward a more physiologically and evolutionarily relevant definition of metal hyperaccumulation in plants. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2015.00554>
- van der Ent A, Rajakaruna N, Boyd R et al (2015b) Global research on ultramafic (serpentine) ecosystems (8th International Conference on Serpentine Ecology in Sabah, Malaysia): a summary and synthesis. *Aust J Bot* 63:1–16. <https://doi.org/10.1071/BT15060>
- van der Ent A, Ocenar A, Tisserand R et al (2019) Herbarium X-ray fluorescence screening for nickel, cobalt and manganese hyperaccumulator plants in the flora of Sabah (Malaysia, Borneo Island). *J Geochem Explor* 202:49–58. <https://doi.org/10.1016/j.gexplo.2019.03.013>
- van der Ent A, Joseph Pollard A, Echevarria G et al (2021) Exceptional uptake and accumulation of chemical elements in plants: extending the hyperaccumulation paradigm. In: van der Ent A, Baker AJM, Echevarria G et al (eds) *Agromining: farming for metals: extracting unconventional resources using plants*. Springer International Publishing, Cham, pp 99–131
- Vergnano Gambi O, Gabrielli R (1979) Ecophysiological and geochemical aspects of nickel, chromium and cobalt accumulation in the vegetation of some Italian ophiolitic outcrops. *Ofioliti*:199–208
- Violle C, Navas M-L, Vile D et al (2007) Let the concept of trait be functional! *Oikos* 116:882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Violle C, Borgy B, Choler P (2015) Trait databases: misuses and precautions. *J Veg Sci* 26:826–827. <https://doi.org/10.1111/jvs.12325>
- Whiting SN, Reeves RD, Richards D et al (2004) Research priorities for conservation of metallophyte biodiversity and their potential for restoration and site remediation. *Restor Ecol* 12:106–116. <https://doi.org/10.1111/j.1061-2971.2004.00367.x>
- Wójcik M, Gonnelli C, Selvi F et al (2017) Metallophytes of serpentine and calamine soils – their unique ecophysiology and potential for phytoremediation. In: Cuypers A, Vangronsveld J (eds) *Phytoremediation*. Academic Press, pp 1–42
- Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827. <https://doi.org/10.1038/nature02403>

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.