Received: 15 November 2023 | Revised: 5 April 2024 | Accepted: 11 April 2024
DOI: 10.1111/1440-1703.12479

NOTES AND INSIGHTS

Ultramafic Ecology: Proceedings of the 10th International Conference on Serpentine Ecology

Can vermicomposting be used to process hyperaccumulator biomass in nickel agromining?

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Funding information
Xunta de Galicia, Grant/Award Number: ED431C 2022/07; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 892814; Ministerio de Ciencia e Innovación, Grant/Award Numbers: PID2021-124265OB-100, TED2021-129437B-100

Abstract

Hyperaccumulator plants are a botanical curiosity that have allowed the development of agromining of metals, with a special focus on nickel. In nickel agromining, this element is recovered from ashed hyperaccumulators cultivated on metal-rich soils. In order to explore bio-based approaches for the decomposition of hyperaccumulator biomass and nickel recovery that do not include burning, we performed a vermicomposting experiment using the earthworm species *Eisenia andrei* and the biomass of *Bornmuellera emarginata* (which contained almost 1% of nickel). We conducted our experiment for 12 weeks and assessed the decomposition process of the hyperaccumulator biomass, changes in earthworm number and biomass, and changes in nickel concentration and mobility. Despite the initial mortality and an increase of Ni concentration in earthworm tissues, *E. andrei* was able to decompose *B. emarginata* biomass. This process also showed a massive colonization of the biomass by a fungus during the first weeks of the assay. Our results indicate that the vermicomposted hyperaccumulator biomass had a higher nickel concentration than the starting material but the diethylenetriaminepentaacetic acid-extractable nickel decreased. At the same time, due to earthworm activity, the nickel was redistributed and diluted in the vermicompost bedding, reducing the interest of this approach for agromining, but opening the perspective of using the vermicomposted hyperaccumulator biomass as an organic amendment in nickel-deficient crops.

KEYWORDS

Bornmuellera emarginata, decomposition, earthworms, *Eisenia andrei*, Ni mobility

1 | INTRODUCTION

Metal hyperaccumulators are plants that are able to actively take up and store in their leaves concentrations of trace elements that are 2–3 orders of magnitude higher than plant leaves on normal soils or at least one order of magnitude greater than plant leaves on metalliferous soils (van der Ent, Baker, Reeves, et al., 2013). To date, more than 700 species have been described as metal hyperaccumulators, 70% of which hyperaccumulate nickel (Reeves et al., 2018).

In addition to being model organisms for the study of plant evolution or plant tolerance to extreme conditions (e.g., García de la Torre et al., 2021; Jaffré et al., 2013; Krämer, 2010; Rascio & Navari-Izzo, 2011), metal hyperaccumulators have served as the basis for development of soil remediation by phytoextraction and, more recently, phytomining and agromining (i.e., the cultivation of hyperaccumulator plants in post-mining landscapes or in marginal and low productive metal-rich agricultural areas to extract valuable metals from soil for an economic profit) (Bani et al., 2007; Chaney et al., 2018; Kidd et al., 2018; Nkrumah et al., 2016).

The economic feasibility of agromining and phytomining depends on several factors: the market value of the extracted metal, the occurrence of hyperaccumulators with high metal concentration and/or high biomass, and the availability of metal-rich land surface (Chaney et al., 2018; Nkrumah et al., 2016; Van der Ent et al., 2015; Van der Ent, Baker, Van Balgooy, & Tjoa, 2013). Thus, nickel is the element for which research in agromining is more advanced (Chaney et al., 2018; Kidd et al., 2018; Nkrumah et al., 2016) and harvests higher than 100 (or even 200) kg of Ni per hectare have been obtained in temperate and tropical areas (Bani et al., 2015; Nkrumah et al., 2016; Tisserand et al., 2021). Recently, two EU-funded projects (Agronickel and Life-Agromine) explored the selection of adequate nickel crops and the optimization of biomass production and Ni extraction/recovery, as well as establishing a network of agromining fieldscale plots where the environmental and socioeconomic viability of agromining could be demonstrated (Kidd et al., 2018). These projects were based on the use of several hypernickelophores (i.e., species where Ni concentration in biomass was higher than 1%) such as *Odontarrhena chalcidica* (previously identified as *Alyssum murale*) or *Bornmuellera emarginata* (previously identified as *Leptoplax emarginata*) (Kidd et al., 2018; Nkrumah et al., 2016). Once harvested and dried, Ni can be leached from the hyperaccumulator biomass (Guilpain et al., 2018), but more commonly the biomass is burnt and the Ni (or a Ni-including compound) is recovered from the ashes by hydrometallurgy (Barbaroux et al., 2012; Simmonot et al., 2018).

To test the feasibility of biological processes for the decomposition of hyperaccumulators biomass and nickel recovery, we conducted a vermicomposting experiment using biomass of the nickel hyperaccumulator *B. emarginata*. Vermicomposting is a bio-oxidative process in which detritivore earthworms interact intensively with microorganisms and other soil fauna to accelerate the stabilization of organic matter and greatly modify its physical and biochemical properties (Domínguez, 2004, 2023). Through comminution, burrowing, and casting the earthworms increase the organic matter surface that is available for the decomposing activity by microorganism communities, resulting in an overall stimulation of organic matter decomposition (Blouin et al., 2013; Domínguez et al., 2010; Lavelle & Spain, 2001). Vermicomposting procedures make use of several epigeic (i.e., "litter-dwelling") earthworm species with interesting traits such as high rates of consumption of organic matter, wide tolerance of environmental factors, or high-reproductive rates (Domínguez & Edwards, 2010). To date, vermicomposting systems have been applied to the decomposition and stabilization of various organic residues and plant biomass (e.g., Domínguez, 2023; Domínguez et al., 2018; Ferraz Ramos et al., 2022; Gómez-Brandón & Domínguez, 2014; Quintela-Sabarís et al., 2022; Sánchez-Hernández & Domínguez, 2019).

Several studies have explored the processing of metal-rich substrates (such as sewage sludge) with earthworms aiming at organic matter stabilization and/or the transformation of the substrates into high-quality fertilizers (see Swati and Hait (2017) for a review). In general, earthworms were able to decompose those substrates, but concentrations and the bioavailability of metals in the vermicomposted biomass increased or decreased depending on the feedstock and co-substrates or the metal considered (Swati & Hait, 2017). For instance, Singh and Kalamdhad (2013) showed that the vermicomposting of raw water hyacinth increased nickel bioavailability whereas vermicomposting a mixture of water hyacinth with cattle manure and/or sawdust reduced Ni bioavailability. To our knowledge, there is no previous experience on the vermicomposting of extremely metal-rich hyperaccumulator biomass (where metal concentrations may reach 1% of biomass dry weight [DW]). Thus, our experiment will allow us to evaluate the capacity of earthworms to colonize and process hyperaccumulator biomass and determine whether vermicomposting increases or reduces the nickel mobility.

2 | MATERIALS AND METHODS

2.1 | Plant material

Dry, Ni-rich shoot biomass of the hyperaccumulator *B. emarginata* was provided by Dr Ángeles Prieto-Fernández and Dr. Beatriz Rodríguez Garrido (MBG-CSIC, Spain). The plants came from an experimental agromining fieldplot near Eidián (Galicia, NW Spain), which is part of a European network of agromining field sites. More information on the Eidián fieldplot and other sites in the network can be found in Kidd et al. (2018). Dry shoots were cut into fragments of 1–2 cm. The day the experiment began, the fragmented plant biomass was moisturized with distilled water to reach an 80% moisture content.

2.2 | Earthworms and bedding material

We collected 5 kg of vermicompost produced in the facilities of the Animal Ecology research group (University of Vigo Campus, Vigo, Spain). The vermicompost was used as earthworm bedding and was produced from distilled grape marc, which was processed by the earthworm species *Eisenia andrei* in a medium-sized plastic vermirreactor (dimensions 1.18 × 0.6 × 1 m). Prior to the experimental set-up, we carefully screened the vermicompost to remove any remaining *E. andrei* individuals and cocoons. *Eisenia andrei* (Bouché) is a ubiquitous earthworm species, and one of the most commonly used in vermicomposting (Domínguez, 2023; Domínguez et al., 2019; Domínguez & Edwards, 2010; Ferraz Ramos et al., 2022).

2.3 | Experimental set-up

The experiment was conducted in 750-mL polystyrene boxes. Each box was filled with a bedding layer of 200 g (fresh weight [FW]) of vermicompost free of earthworms. Then, 30 individuals of *E. andrei* (total FW 10 ± 0.5 g) were added to each box. This is equivalent to a density of 5000 earthworms m^{-2}, which is a standard value in vermirreactors, where densities may reach between 8000 and 20,000 individuals m^{-2} (Domínguez, 2023; Monroy et al., 2006). A layer of 70 g (FW) of ground *B. emarginata* biomass was placed over a plastic mesh (5 cm mesh size) to allow the separate collection of bedding material and processed biomass at the end of the experiment.

To follow-up the vermicomposting process, boxes were destructively sampled at the beginning of the trial (Day 0) and after 4, 8, and 12 weeks. There were 4 replicated boxes per sampling time, giving a total of 16 boxes. During the experiment, boxes were kept in the dark in a culture chamber with a constant temperature of 22°C. Moisture in the boxes was controlled twice per week by adding distilled water if needed to keep moisture content at around 80%. The position of the boxes inside the growth chamber was randomized once per week. During the first 2 weeks, the surface of the vermicompost bedding layer was inspected three times per week to monitor earthworm mortality and any dead earthworms were removed (no new earthworms were added).

2.4 | Experiment harvesting

Four boxes were harvested per sampling time. Each box was processed as follows: the layers above (worm-worked plant biomass, hereafter "biomass") and below (earthworm bedding, hereafter "vermicompost") the plastic mesh were collected separately and screened for the presence of earthworms and cocoons. Earthworms were collected, rinsed with distilled water to remove adhering particles and put in Petri dishes between two layers of filter paper, previously moisturized with distilled water. Petri dishes with earthworms were kept in the dark at room temperature for 24 h to allow the earthworms to empty their guts. Earthworm casts (gut contents) were collected with a small spoon and transferred to Eppendorf tubes and dried at 60°C overnight. Due to the small amount of casts collected, we grouped them by sampling time, giving a total of four dry earthworm cast samples. Then, earthworms were collected, counted, rinsed again with distilled water, gently blotted with paper tissue, and weighed to obtain total earthworm FW per box and dried at 60°C until constant weight, giving one dry earthworm sample per box. Once the earthworms were removed from the biomass and the vermicompost bedding, we obtained the FW and we used a small subsample to measure moisture content and then estimate the DW of each fraction. Afterwards, biomass and vermicompost were divided into two subsamples: one subsample was stored at −80°C to perform microbiological analyses whereas the other subsample was dried at 60°C until constant weight and used for physicochemical analyses.

2.5 | Sample analysis

The pH and electrical conductivity (EC) of biomass and vermicompost were estimated in aqueous extracts (1:10 weight to volume) using a Crison MicropH 2000 pH meter and a Crison CM35 conductivity meter, respectively. Basal respiration was estimated from CO_2 production. Frozen subsamples of biomass and vermicompost were removed from the freezer and kept in the dark at 20°C for 1 week in order to allow the microbiota to resume its activity. Afterwards, 5 g (FW) of each subsample were placed in 100-mL glass vessels, which were then hermetically sealed and incubated at 22°C for 6 h. The CO_2 produced from the sample was trapped in 0.02 M NaOH and CO_2 production was quantified by titration with 0.01 M HCl to a phenolphthalein endpoint after the addition of excess $BaCl_2$ (Anderson, 1983). Total C and N contents in biomass were determined in dried samples in a Carlo Erba EA 1108 CHNS-O 1500 C/N analyzer. The chemical composition of vermicompost, biomass, casts, and earthworms was determined in dry ground subsamples. Each subsample (0.2 g) was placed in a Teflon container (Savillex) to which 4 mL HNO_3, 1 mL Hcl, and 2 mL H_2O_2 were added. Samples were digested in a microwave oven (Anton Paar-GmbH Multiwave-3000) at 800 W for 45 min. Samples were left to cool down and diluted to 50 mL using MilliQ water. The pseudototal concentrations of Ni, Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn were quantified in digested samples by inductively coupled plasma optical emission spectroscopy (iCAP-PRO XP Duo analyzer, Thermo Fisher, Madison, WI, USA). Nickel mobility in plant biomass and vermicompost was evaluated after extraction with DTPA-TEA (0.005 M diethylenetriaminepentaacetic acid [DTPA] with 0.01 M $CaCl_2$ and 0.1 M triethanolamine [TEA] at pH 7.3, 1:15 w/v, 2 h shaking) (Lindsay & Norvell, 1978). The molecular structure of primary and secondary compounds of hyperaccumulator biomass was determined by Fourier transform infrared spectroscopy combined with attenuated total reflectance (FTIR-ATR) (in a Thermo Nicolet 6700 spectrometer equipped with a Smart Orbit Diamond ATR accessory, Thermo Fisher). FTIR-ATR spectra were acquired at a resolution of 4 cm^{-1} in the mid-infrared region (4000–400 cm^{-1}) by averaging 32 scans per sample. Infrared spectra were processed using the `andurinha` package (Álvarez-Fernández & Martínez-Cortizas, 2020) in R version 4.2.2 (R Core Team, 2022). This package computes the mean absorbance spectrum and the standard deviation spectrum (to check for regions of the spectra with higher variability among samples). It also provides the second derivative spectra that we used to identify relevant peaks. To assign the identified peaks to functional groups and/or putative chemical compounds, we used information provided by Artz et al. (2008), Carballo et al. (2008), Oberle et al. (2015), Srivastava et al. (2020) and Martínez Cortizas et al. (2021).

2.6 | Data analysis

Variation with time in plant biomass DW, all the chemical and microbiological parameters in plant biomass, and the variation of total earthworm FW were assessed by one-way analysis of variances (ANOVAs) followed by post hoc Tukey tests to identify significant differences between conditions. Variation in earthworm number with time was evaluated using a linear model with a Poisson distribution followed by a post hoc Tukey test using packages `emmeans` (Lenth, 2023) and `multcompView` (Graves et al., 2023), in R (ver. 4.2.2) (R Core Team, 2022).

Variation of pseudototal nickel concentrations in plant biomass, vermicompost, and earthworms, and the DTPA-extracted Ni in biomass and vermicompost with time was assessed by one-way ANOVAs. Variation in Ni distribution between compartments (biomass, vermicompost, earthworms, and casts) with time was estimated using the values of pseudototal Ni concentrations and the DW of each compartment.

When required, variables were transformed (log10 or power transformation) to meet the ANOVA assumption of homocedasticity. ANOVAs and post hoc tests were computed using SPSS (v. 15, SPSS Inc., Chicago, IL, USA). Variables that after transformation did not meet ANOVA requirements were analyzed by the nonparametrical Kruskal–Wallis test, followed by a Dunn test for multiple comparisons using the package `PMCMRplus` (ver 1.9.7) (Pohlert, 2023) in R (ver. 4.2.2) (R Core Team, 2022).

3 | RESULTS

Vermicomposting resulted in a biomass loss of around 58% after 12 weeks, moving from 20 g DW at Time 0 to an average of 8.48 g DW of biomass at the end of the experiment (12 weeks, Figure 1a). The strongest mass loss occurred from Time 0 to Week 4, and from this point mass loss continued at a slower pace. During the first 2 weeks of the experiment, hyperaccumulator biomass was strongly colonized by a layer of a greenish-bluish mold, and during that time the earthworms were found mainly in the vermicompost bedding layer or in the interface between the vermicompost and the hyperaccumulator biomass. Earthworm mortality during the first 2 weeks ranged between 0% and 20%, but in one box all the earthworms died (100% mortality) and this box was not included in our analyses. The number and biomass of earthworms decreased from Time 0 to Week 4 (a decrease of around 50% in earthworm number and 75% decrease in earthworm FW), and then these parameters were stable during the rest of the experiment (Figure 1b,c).

Bornmuellera emarginata biomass at the beginning of the experiment had a pH near neutrality, a relatively high EC, and remarkable concentrations of Ca (15.96 g kg^{-1}), K (22.66 g kg^{-1}), and S (6.83 g kg^{-1}). Average cobalt (Co) concentration was 30.02 mg kg^{-1} (Table 1). Vermicomposting induced important changes in the chemical and microbiological parameters of the plant material. The pH increased during vermicomposting, reaching values higher than 9 on Week 12 (Table 1). In contrast, EC and basal respiration decreased from Week 0 to Week

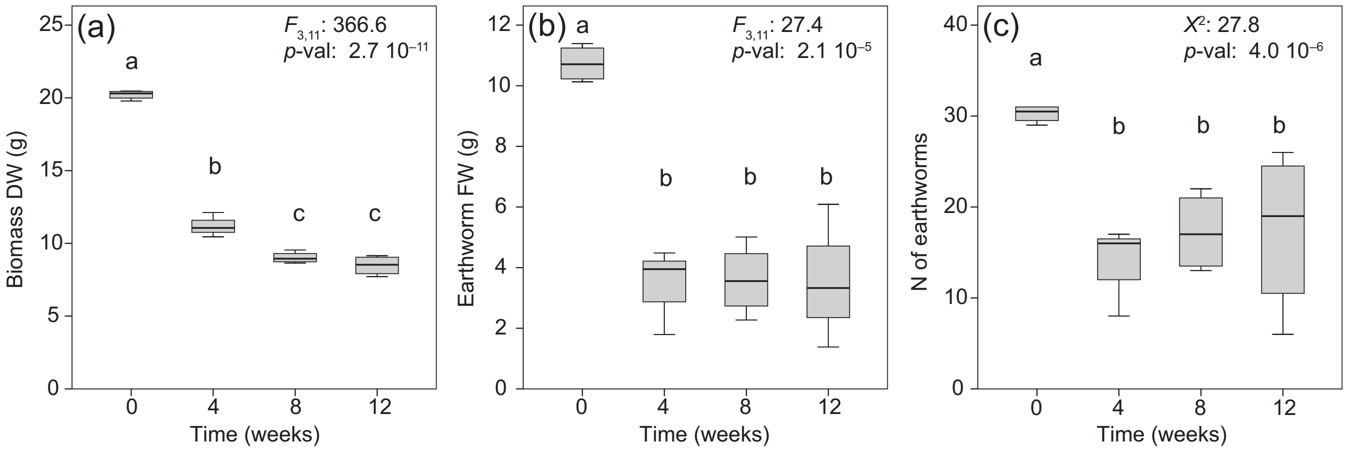

FIGURE 1 Variation in the biomass dry weight (DW) of the Ni-hyperaccumulator *Bornmuellera emarginata* (a) and in the fresh weight (FW) (b), and number of individuals (c) of the earthworm *Eisenia andrei* during 12 weeks of a vermicomposting experiment of the hyperaccumulator biomass. In each plot, the bottom and top of each box indicate the first and third quartiles, and the band inside the box marks the median for each sampling time. In each plot, different letters indicate significant differences between sampling times. The values of *F* and X^2 statistics for the factor time, as well as the *p*-values of each test are indicated on the top-right corner of each plot.

12. Carbon and nitrogen concentration in the biomass remained stable during the experiment (values around 40% and 3%, respectively), whereas other chemical elements (with the exception of S and Zn) increased in concentration during vermicomposting (Table 1).

The analysis of FTIR-ATR data allowed us to identify 8 peaks at wavenumbers 1514 cm^{-1} (related to lignin), 1981, 2050, 2146, 2164, and 2324 cm^{-1} (related to the C—N triple bonds in alkynes) and 2850 and 2920 cm^{-1} (related to fats, waxes, and lipids). Six out of the eight IR peaks were unaffected by vermicomposting, whereas the scaled absorbance of the peak at wavenumber 1514 cm^{-1} increased from Time 0 to Week 12, and the absorbance of the peak at wavenumber 2920 cm^{-1} decreased from Time 0 to Week 4 and then increased to values similar to Time 0 (Table 1).

The pseudototal nickel concentrations in biomass, vermicompost, and earthworms at the beginning of the experiment were 9028 ± 310, 248 ± 66 and 22 ± 30 mg kg^{-1} DW, respectively. This parameter increased significantly with time for biomass and for earthworms to 11,598 ± 947 and 147 ± 48 mg kg^{-1} DW, respectively. Pseudototal Ni concentration in the vermicompost after 12 weeks was 1818 ± 410 mg kg^{-1} DW, although it was not different from Time 0, according to the Kruskal–Wallis test (Figure 2a). The Ni pseudototal concentration in the casts was 80.5 mg kg^{-1} DW at the beginning of the experiment and 4465 mg kg^{-1} DW at the end of the experiment, with the highest values (more than 11,500 mg kg^{-1} DW) at Weeks 4 and 8 (Figure 2a). However, as we only had one sample of casts per time, we could not assess the statistical significance of this variation.

DTPA-extractable Ni concentrations (hereafter, Ni-DTPA) in biomass was 8064 ± 1046 mg kg^{-1} DW at the beginning of the experiment and decreased to a value of 5904 ± 476 mg kg^{-1} DW at Week 12. In the vermicompost, Ni-DTPA increased from 172 ± 37 mg kg^{-1} DW at Time 0 to 1001 ± 192 mg kg^{-1} DW at the end of the trial (Figure 2b).

The absolute amount of Ni in each box was 191.8 ± 30.3 g. At Time 0, most of this nickel (92.4%) was contained in plant biomass, whereas the vermicompost stored only 7.6% (Figure 2c). During the experiment there was a redistribution of the nickel, with a continuous decrease of the metal stored in the worm-worked plant biomass and a continuous increase of metal in the vermicompost bedding. Thus, at Week 12, 52.0% of the nickel was in the vermicompost whereas the biomass contained 47.9% (Figure 2c). Despite the high Ni concentrations in the earthworms and especially in the casts, the low DW of those fractions made the percentages of Ni in earthworms and casts quite small (0.03% and 0.07%, respectively).

4 | DISCUSSION

In this experiment we explored the application of the earthworm *E. andrei* for the decomposition of biomass of the hypernickelophore *B. emarginata* for nickel recovery from agromining.

Our analyses showed that after 12 weeks *E. andrei* (and associated microorganisms) were able to decompose the *B. emarginata* biomass, resulting in an important reduction in DW and the modification of several

TABLE 1 Summary of the chemical and microbiological parameters of the vermicompost (VC) at Time 0 and the *Bornmuellera emarginata* biomass (B) after 0, 4, 8, and 12 weeks of vermicomposting procedure with *Eisenia andrei*.

Variables	VC (Time 0)	B (Time 0)	B (Time 4)	B (Time 8)	B (Time 12)
pH	8.45 ± 0.12	6.93 ± 0.68^{b}	8.78 ± 0.07^{ab}	8.84 ± 0.12^{ab}	9.09 ± 0.08^{a}
EC (mS cm^{-1})	359 ± 53	1882 ± 541^{a}	707 ± 95^{ab}	724 ± 42^{b}	789 ± 48^{ab}
C (%)	48.7 ± 2.3	39.4 ± 0.4^{a}	39.4 ± 0.2^{a}	37.8 ± 2.2^{a}	40.1 ± 2.9^{a}
N (%)	2.24 ± 0.67	2.34 ± 0.1^{a}	3.17 ± 0.48^{a}	3.02 ± 0.30^{a}	3.19 ± 0.12^{a}
Basal respiration (μg CO_2 g^{-1} DW h^{-1})	566 ± 60	2340 ± 514^{a}	1041 ± 79^{ab}	724 ± 60^{ab}	545 ± 21^{b}
Pseudototal concentrations of major elements (g kg^{-1})					
Al	0.3 ± 0.0	0.2 ± 0.0^{b}	0.5 ± 0.0^{ab}	0.5 ± 0.1^{a}	0.4 ± 0.1^{ab}
Ca	5.3 ± 0.3	16.0 ± 0.6^{b}	24.6 ± 2.2^{a}	26.9 ± 1.7^{a}	26.7 ± 2.9^{a}
K	20.4 ± 1.5	22.7 ± 0.5^{c}	29.3 ± 1.6^{b}	33.8 ± 1.0^{a}	30.9 ± 2.0^{ab}
Mg	1.4 ± 0.2	2.3 ± 0.0^{c}	2.7 ± 0.2^{b}	3.1 ± 0.1^{a}	3.4 ± 0.2^{a}
Na	1.7 ± 0.1	0.4 ± 0.0^{b}	2.2 ± 0.3^{ab}	2.7 ± 0.3^{a}	2.7 ± 0.3^{a}
P	3.1 ± 0.4	3.2 ± 0.1^{c}	7.8 ± 0.9^{b}	11.0 ± 0.3^{a}	11.2 ± 1.5^{a}
S	1.9 ± 0.2	6.8 ± 0.1^{a}	4.9 ± 0.3^{b}	4.7 ± 0.3^{b}	4.9 ± 0.1^{b}
Pseudototal concentrations of trace elements (mg kg^{-1})					
Co	1.0 ± 0.3	30.0 ± 2.1^{b}	46.8 ± 4.4^{a}	45.9 ± 2.2^{a}	43.6 ± 4.4^{a}
Cr	2.5 ± 0.8	3.5 ± 0.7^{b}	17.4 ± 1.3^{a}	11.4 ± 0.8^{ab}	15.2 ± 5.7^{ab}
Cu	119.7 ± 16.7	4.2 ± 0.2^{c}	22.7 ± 7.9^{bc}	34.1 ± 12.3^{b}	70.8 ± 16.2^{a}
Fe	273.3 ± 46.3	217.0 ± 18.3^{b}	628.0 ± 18.7^{a}	608.5 ± 39.5^{a}	615.3 ± 23.2^{a}
Mn	33.0 ± 4.0	91.0 ± 6.0^{b}	165.0 ± 13.0^{a}	178.0 ± 8.0^{a}	174.0 ± 14.0^{a}
Zn	17.9 ± 1.5	45.6 ± 5.5^{a}	105.5 ± 56.9^{a}	82.2 ± 3.5^{a}	83.2 ± 11.4^{a}
FTIR-ATR peaks (second derivative absorbances scaled as *Z*-scores)					
WN1514	nd	-0.068 ± 0.013^{b}	0.791 ± 0.035^{ab}	0.829 ± 0.029^{a}	0.773 ± 0.084^{ab}
WN1981	nd	-0.806 ± 0.027^{a}	-0.758 ± 0.022^{a}	-0.803 ± 0.024^{a}	-0.764 ± 0.034^{a}
WN2050	nd	-0.786 ± 0.019^{a}	-0.750 ± 0.037^{a}	-0.777 ± 0.026^{a}	-0.740 ± 0.039^{a}
WN2146	nd	-1.003 ± 0.007^{a}	-0.951 ± 0.064^{a}	-0.959 ± 0.016^{a}	-0.973 ± 0.019^{a}
WN2164	nd	-0.798 ± 0.018^{a}	-0.741 ± 0.071^{a}	-0.733 ± 0.014^{a}	-0.733 ± 0.054^{a}
WN2324	nd	-0.733 ± 0.032^{a}	-0.721 ± 0.011^{a}	-0.679 ± 0.060^{a}	-0.699 ± 0.036^{a}
WN2850	nd	0.786 ± 0.036^{a}	0.911 ± 0.087^{a}	0.855 ± 0.094^{a}	0.828 ± 0.059^{a}
WN2920	nd	1.427 ± 0.062^{b}	1.712 ± 0.098^{a}	1.624 ± 0.132^{ab}	1.539 ± 0.098^{ab}

Note: For each sampling time, we present the mean ± standard deviation ($n = 4$). For each row, different superscript letters in the biomass time categories indicate significant differences as indicated by Tukey post hoc analyses ($p < 0.05$). Basal respiration at Time 0 is actually at Time 1, since the samples were left to equilibrate for 1 week after being removed from the freezer (see Section 2).

Abbreviation: nd, not determined.

chemical (increase in pH and lignin, decrease in EC) and biological (decrease in basal respiration) parameters. Final DW (at Week 12) of the worm-worked biomass was around 40% of the biomass at Time 0. Biomass loss occurred mainly during the first 4 weeks of the experiment and decomposition progressed at a slower pace from Week 4 to Week 12. This pattern follows the model of litter decomposition proposed by Berg and Matzner (1997) who identified two phases: an initial stage in which rapid decomposition of more labile compounds occurs and a later stage in which the accumulation of lignin and other recalcitrant compounds reduces the decomposition rate. Thus, our FTIR results showed an increase in lignin abundance with vermicomposting time and a relative decrease in cellulose and hemicellulose as has been observed during the vermicomposting of other plant litters (e.g., Domínguez et al., 2018; Quintela-Sabarís et al., 2022).

Basal respiration in our experiment also followed the rhythm of litter decomposition, with high values on Week 0 and Week 4. This maximum in respiration coincided with the massive growth of fungi on the plant

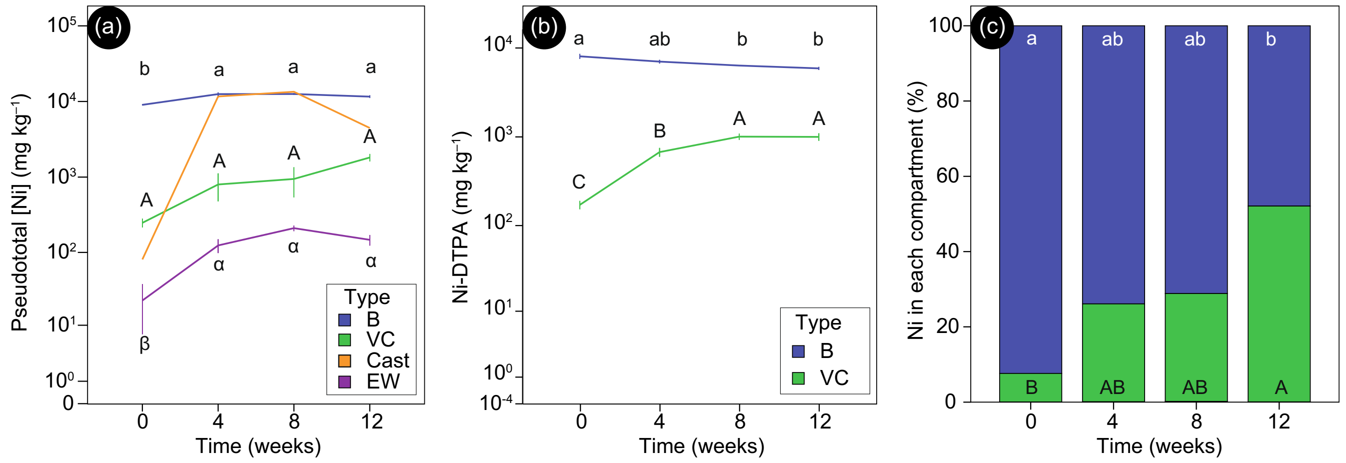

FIGURE 2 Variation in the pseudototal Ni concentration (a), DTPA-extractable Ni concentration (b) and absolute Ni distribution between compartments (c) during 12 weeks of a vermicomposting experiment of the hyperaccumulator *Bornmuellera emarginata* with the epigeic earthworm *Eisenia andrei*. In (a) and (b), the *y*-axis is on logarithmic scale, and the lines indicate the mean values for each compartment, whereas the whiskers denote the standard error. Each compartment is indicated by a different color: blue (biomass, B), green (vermicompost bedding, VC), orange (casts) and purple (earthworm, EW). Due to the small percentage of Ni stored in earthworms and casts, these compartments are not visible in (c). In each plot, different letters indicate significant differences (p-val <0.05) between sampling times for each compartment (lowercase letters, B; capital letters, VC bedding; Greek letters, EWs—only in (a)), according to Tukey or to Dunn post hoc tests with correction for multiple comparisons.

biomass during the first weeks of the experiment. From that point, there was a progressive reduction in basal respiration. The reduction of basal respiration with time is common during vermicomposting and is related to the progressive reduction of easy-to-degrade biomass and the accumulation of recalcitrant compounds, which also induces changes in the composition of the bacterial communities (Domínguez et al., 2010, 2014, 2019; Ferraz Ramos et al., 2022; Gómez-Brandón et al., 2020).

In parallel to the dry matter loss and the decrease in basal respiration, the EC of the vermicomposted *B. emarginata* biomass was lower than in the initial biomass. Decreased EC during the composting and vermicomposting of organic wastes has been related to a drop in soluble ion concentrations due to leaching because of biomass irrigation, immobilization by the microorganisms or earthworms, chelation by newly formed organic compounds or precipitation in the form of non-soluble salts (Domínguez et al., 2018; Fornes et al., 2012; Huang et al., 2014). In our experiment, leaching from the hyperaccumulator biomass to the vermicompost bedding could be responsible for part of the reduction in EC. However, the fact that the concentration of all the chemical elements (with the exception of C and N) increased in the worm-worked biomass suggests that the chelation of mineral elements by complex organic compounds in the worm-worked biomass may be responsible for part of the decrease in EC.

Focusing on nickel, our results showed important changes in the concentration, mobility, and distribution of this element between the studied compartments. As we observed for other elements, the pseudototal Ni concentration in the worm-worked hyperaccumulator biomass slightly increased compared to the original biomass, whereas the Ni-DTPA decreased. This pattern is consistent with nickel chelation by vermicomposted organic matter (Swati & Hait, 2017). At the same time, the Ni-DTPA in the vermicompost bedding increased and the pseudototal concentration of this element in the bedding material also showed a trend of increasing. During the first 2 weeks of the experiment, the movement of nickel between compartments could be due to leaching, because we did not observe colonization of the hyperaccumulator biomass by the earthworms. However, the increased concentrations of nickel in the earthworms' bodies and in the casts at 4, 8, and 12 weeks indicate that *E. andrei* was able to ingest and digest the nickel-rich *B. emarginata* biomass and, thus, mix the biomass with the vermicompost bedding. The balance of this process resulted in a dilution of the nickel in a higher amount of organic matter (worm-worked biomass + bedding), which makes nickel recovery more difficult and unfeasible for agromining.

Several studies have assessed the effect of vermicomposting not only on metal bioavailability, but also on metal concentration in different organic wastes (Sánchez-Hernández & Domínguez, 2019; Swati & Hait, 2017). The loss of weight of the organic waste due to the decomposition of the organic compounds usually led to an increase in metal concentrations (as we observed in our experiment), but some studies have reported a net reduction in metal concentration in vermicomposted biomass, which was attributed to the bioaccumulation of metal in the earthworms' tissues (Swati & Hait, 2017). However, in these other studies metal concentrations in the vermicomposted substrates were quite lower (ranging between 0.01 and 500 mg kg^{-1} Ni, e.g., Domínguez-Crespo et al., 2012; Singh & Kalamdhad, 2013; Swati & Hait, 2017) than the metal concentrations in hyperaccumulators, so it is possible that the high nickel concentration in *B. emarginata* biomass (almost 1% in our experiment) exceeds the bioaccumulation capacity of *E. andrei* individuals. Thus, in our experiment, the Ni concentration in earthworm tissues showed a sevenfold increase from Day 0 to Week 12 (22 and 150 μg g^{-1}, respectively). These values are higher than the highest Ni concentration in earthworms reported in the literature (86.5 μg g^{-1} quantified in the endogeic—i.e., earth dwelling—earthworm species *Aporrectodea caliginosa* exposed to an ultramafic mine soil; Maleri et al., 2008) and higher than the highest Ni concentration reported from an epigeic earthworm (64.7 μg g^{-1} quantified in *Dendrobaena veneta* exposed to metal-spiked sewage sludge; Natal-da-Luz et al., 2011). Thus, despite an initial reduction in earthworm numbers, *E. andrei* showed an important degree of metal accumulation, but also a high metal tolerance, as the casts secreted by the earthworms reached nickel concentrations of around 1%.

In summary, our research showed that the earthworm *E. andrei* can decompose biomass of the hyperaccumulator *B. emarginata* but vermicomposting decreased nickel mobility and diluted the metal with the bedding material, reducing the interest of this approach for agromining. However, this Ni-rich worm-worked biomass offers new possibilities, such as the use of this material as an organic amendment in Ni-deficient crops. Some crops, such as the pecan tree or legumes may suffer nickel deficiency (or reduced growth with deficiency symptoms) when cultivated on Ni-poor soils or in soils where other elements interfere with nickel absorption (Eskew et al., 1983; Wood et al., 2006). Several studies have shown that fertilization with Ni can increase nitrogen assimilation and nitrogen status in several crops (e.g., Khoshgoftarmanesh et al., 2011; Tan et al., 2000) and can also increase the biomass and/or grain yield of legumes such as soybean (Barman et al., 2020; Siqueira Freitas et al., 2018). Future perspectives include (i) the isolation and identification of the microorganisms (mainly fungi) that profusely colonized the hyperaccumulator biomass for its use in bioreactors, and (ii) the testing of different mixtures of vermicomposted hyperaccumulator biomass on the yield of legume crops.

ACKNOWLEDGMENTS

This research and CQS contract were funded by the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement no. 892814. J.D. acknowledges funding by the Spanish Ministerio de Ciencia e Innovación (PID2021-124265OB-100), the Xunta de Galicia (ED431C 2022/07), and by the MCIN/AEI and European Union Next Generation_EU under the project TED2021-129437B-100. The authors also acknowledge Paul Fraiz for assistance with language editing. Funding for open access charge: Universidade de Vigo/CISUG.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset supporting this publication is openly available online at Zenodo: https://doi.org/10.5281/zenodo.10131336 (accessed on November 15, 2023).

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REFERENCES

Álvarez-Fernández N, Martínez-Cortizas A (2020). *andurinha: Make spectroscopic data processing easier*. R package version 0.02. https://CRAN.R-project.org/package=andurinha

Anderson, J. P. (1983). Soil respiration. In A. L. Page (Ed.), *Methods of soil analysis: Part 2 chemical and microbiological properties* (pp. 831–871). Wiley Online Library.

Artz, R. R., Chapman, S. J., Robertson, A. J., et al. (2008). FTIR spectroscopy can be used as a screening tool for organic matter quality in regenerating cutover peatlands. *Soil Biology and Biochemistry*, *40*, 515–527.

Bani, A., Echevarria, G., Sulçe, S., & Morel, J. L. (2015). Improving the agronomy of *Alyssum murale* for extensive phytomining: A five-year field study. *International Journal of Phytoremediation*, *17*, 117–127. https://doi.org/10.1080/15226514.2013.862204

Bani, A., Echevarria, G., Sulce, S., Morel, J. L., & Mullai, A. (2007). In-situ phytoextraction of Ni by a native population of *Alyssum murale* on an ultramafic site (Albania). *Plant and Soil*, *293*, 79–89.

Barbaroux, R., Plasari, E., Mercier, G., Simonnot, M. O., Morel, J. L., & Blais, J. F. (2012). A new process for nickel ammonium disulfate production from ash of the hyperaccumulating plant *Alyssum murale*. *The Science of the Total Environment*, *423*, 111–119.

Barman, M., Datta, S. P., Rattan, R. K., & Meena, M. C. (2020). Critical limits of deficiency of nickel in intensively cultivated alluvial soils. *Journal of Soil Science and Plant Nutrition*, *20*, 284–292. https://doi.org/10.1007/s42729-019-00141-9

Berg, B., & Matzner, E. (1997). Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Reviews*, *5*, 1–25.

Blouin, M., Hodson, M. E., Delgado, E. A., Baker, G., Brussaard, L., Butt, K. R., Dai, J., Dendooven, L., Peres, G., Tondoh, J. E., Cluzeau, D., & Brun, J. J. (2013). A review of earthworm impact on soil function and ecosystem services. *European Journal of Soil Science*, *64*, 161–182. https://doi.org/10.1111/ejss.12025

Carballo, T., Gil, M. V., Gómez, X., González-Andrés, F., & Morán, A. (2008). Characterization of different compost extracts using Fourier-transform infrared spectroscopy (FTIR) and thermal analysis. *Biodegradation*, *19*, 815–830.

Chaney, R. L., Baker, A. J. M., & Morel, J. L. (2018). The long road to developing agromining/phytomining. In A. Van Der Ent, G. Echevarria, A. J. M. Baker, & J. L. Morel (Eds.), *Agromining: farming for metals* (pp. 1–18). Springer International Publishing.

Domínguez, J. (2004). State-of-the-art and new perspectives on vermicomposting research. In C. A. Edwards (Ed.), *Earthworm ecology* (2nd ed., pp. 401–424). CRC Press.

Domínguez, J. (2023). State-of-the-art and new perspectives on vermicomposting research: 18 years of Progress. In H. A. Mupambwa, L. N. Horn, & P. N. S. Mnkeni (Eds.), *Vermicomposting for sustainable food systems in Africa* (pp. 27–44). Springer.

Domínguez, J., Aira, M., & Gómez-Brandón, M. (2010). Vermicomposting: Earthworms enhance the work of microbes. In H. Insam, I. Franke-Whittle, & M. Goberna (Eds.), *Microbes at work. From wastes to resources* (pp. 93–114). Springer.

Domínguez, J., Aira, M., Kolbe, A. R., Gómez-Brandón, M., & Pérez-Losada, M. (2019). Changes in the composition and function of bacterial communities during vermicomposting may explain beneficial properties of vermicompost. *Scientific Reports*, *9*, 9657. https://doi.org/10.1038/s41598-019-46018-w

Domínguez, J., & Edwards, C. A. (2010). Biology and ecology of earthworm species used for vermicomposting. In C. A. Edwards, N. Q. Arancon, & R. Sherman (Eds.), *Vermiculture technology: Earthworms, organic wastes and environmental management* (pp. 27–40). CRC Press.

Domínguez, J., Gómez-Brandón, M., Martínez-Cordeiro, H., & Lores, M. (2018). Bioconversion of scotch broom into a high-quality organic fertiliser: Vermicomposting as a sustainable option. *Waste Management & Research*, *36*, 1092–1099. https://doi.org/10.1177/0734242X18797176

Domínguez, J., Martínez-Cordeiro, H., Álvarez-Casas, M., & Lores, M. (2014). Vermicomposting grape marc yields high quality organic biofertiliser and bioactive polyphenols. *Waste Management & Research*, *32*, 1235–1240. https://doi.org/10.1177/0734242X14555805

Domínguez-Crespo, M. A., Sánchez-Hernández, Z. E., Torres-Huerta, A. M., Negrete-Rodríguez, M. L. X., Conde-Barajas, E., & Flores-Vela, A. (2012). Effect of the heavy metals Cu, Ni, Cd and Zn on the growth and reproduction of epigeic earthworms (*E. fetida*) during the vermistabilization of municipal sewage sludge. *Water, Air, & Soil Pollution*, *223*, 915–931.

Eskew, D. L., Welch, R. M., & Cary, E. E. (1983). Nickel: An essential micronutrient for legumes and possibly all higher plants. *Science*, *222*, 691–693. https://doi.org/10.1126/science.222.4624.621

Ferraz Ramos, R., Almeida Santana, N., de Andrade, N., Scheffer Romagna, I., Tirloni, B., de Oliveira Silveira, A., Domínguez, J., & Josemar Seminoti Jacques, R. (2022). Vermicomposting of cow manure: Effect of time on earthworm biomass and chemical, physical, and biological properties of vermicompost. *Bioresource Technology*, *345*, 126572. https://doi.org/10.1016/j.biortech.2021.126572

Fornes, F., Mendoza-Hernández, D., García-de-la-Fuente, R., Abad, M., & Belda, R. M. (2012). Composting versus vermicomposting: A comparative study of organic matter evolution through straight and combined processes. *Bioresource Technology*, *118*, 296–305.

García de la Torre, V. S., Majorel-Loulergue, C., Rigaill, G. J., Alfonso-González, D., Soubigou-Taconnat, L., Pillon, Y., Barreau, L., Thomine, S., Fogliani, B., Burtet-Sarramegna, V., & Merlot, S. (2021). Wide cross-species RNA-seq comparison reveals convergent molecular mechanisms involved in nickel hyperaccumulation across dicotyledons. *New Phytologist*, *229*, 994–1006. https://doi.org/10.1111/nph.16775

Gómez-Brandón, M., Aira, M., Santana, N., Pérez-Losada, M., & Domínguez, J. (2020). Temporal dynamics of bacterial communities in a pilot-scale vermireactor fed with distilled grape marc. *Microorganisms*, *8*, 642.

Gómez-Brandón, M., & Domínguez, J. (2014). Recycling of solid organic wastes through vermicomposting: Microbial community changes throughout the process and use of vermicompost as a soil amendment. *Critical Reviews in Environmental Science and Technology*, *44*, 1289–1312. https://doi.org/10.1080/10643389.2013.763588

Graves S, Piepho H, Selzer L, Dorai-Raj S (2023). *multcompView: Visualizations of paired comparisons*. R package version 0.1-9. https://CRAN.R-project.org/package=multcompView

Guilpain, M., Laubie, B., Zhang, X., Morel, J. L., & Simmonot, M. O. (2018). Speciation of nickel extracted from hyperaccumulator plants by water leaching. *Hidrometallurgy*, *180*, 192–200.

Huang, K., Li, F., Wei, Y., Fu, X., & Chen, X. (2014). Effects of earthworms on physicochemical properties and microbial profiles during vermicomposting of fresh fruit and vegetable wastes. *Bioresource Technology*, *170*, 45–52.

Jaffré, T., Pillon, Y., Thomine, S., & Merlot, S. (2013). The metal hyperaccumulators from New Caledonia can broaden our understanding of nickel accumulation in plants. *Frontiers in Plant Science*, *4*, 00279. https://doi.org/10.3389/fpls.2013.00279

Khoshgoftarmanesh, A. H., Hosseini, F., & Afyuni, M. (2011). Nickel supplementation effect on the growth, urease activity and urea and nitrate concentrations in lettuce supplied with different nitrogen sources. *Scientia Horticulturae*, *130*, 381–385. https://doi.org/10.1016/j.scientia.2011.07.009

Kidd, P. S., Bani, A., Benizri, E., Gonnelli, C., Hazotte, C., Kisser, J., Konstantinou, M., Kuppens, T., Kyrkas, D., Laubie, B., Malina, R., Morel, J. L., Olcay, H., Pardo, T., Pons, M. N., Prieto-Fernández, Á., Puschenreiter, M., Quintela-Sabarís, C., Ridard, C., … Echevarria, G. (2018). Developing sustainable agromining systems in agricultural ultramafic soils for nickel recovery. *Frontiers in Environmental Science*, *6*, 00044. https://doi.org/10.3389/fenvs.2018.00044

Krämer, U. (2010). Metal hyperaccumulation in plants. *Annual Review of Plant Biology*, *61*, 517–534.

Lavelle, P., & Spain, A. V. (2001). *Soil ecology*. Kluwer Academic Publishers.

Lenth R (2023). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.8.6. https://CRAN.R-project.org/package=emmeans

Lindsay, W. L., & Norvell, W. A. (1978). Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America Journal*, *42*, 421–428.

Maleri, R. A., Reinecke, A. J., & Reinecke, S. A. (2008). Metal uptake of two ecophysiologically different earthworms (*Eisenia fetida* and *Aporrectodea caliginosa*) exposed to ultramafic soils. *Applied Soil Ecology*, *38*, 42–50.

Martínez Cortizas, A., Sjöström, J. K., Ryberg, E. E., Kylander, M. E., Kaal, J., López-Costas, O., Álvarez Fernández, N., & Bindler, R. (2021). 9000 years of changes in peat organic matter composition in Store Mosse (Sweden) traced using FTIR-ATR. *Boreas*, *50*, 1161–1178. https://doi.org/10.1111/bor.12527

Monroy, F., Aira, M., Domínguez, J., & Velando, A. (2006). Seasonal population dynamics of *Eisenia fetida* (Savigny, 1826) (Oligochaeta, Lumbricidae) in the field. *Comptes Rendus Biologies*, *329*, 912–915. https://doi.org/10.1016/j.crvi.2006.08.001

Natal-da-Luz, T., Ojeda, G., Costa, M., Pratas, J., LAnno, R. P., van Gestel, C. A. M., & Sousa, J. P. (2011). Short-term changes of metal availability in soil. II: The influence of earthworm activity. *Applied Soil Ecology*, *49*, 178–186.

Nkrumah, P. N., Baker, A. J., Chaney, R. L., et al. (2016). Current status and challenges in developing nickel phytomining: An agronomic perspective. *Plant and Soil*, *406*, 55–69.

Oberle, J., Dighton, J., & Arbuckle-Keil, G. (2015). Comparison of methodologies for separation of fungal isolates using Fourier transform infrared (FTIR) spectroscopy and Fourier transform infrared-attenuated total reflectance (FTIR-ATR) microspectroscopy. *Fungal Biology*, *119*, 1100–1114. https://doi.org/10.1016/j.funbio.2015.08.007

Pohlert T (2023). *PMCMRplus: Calculate pairwise multiple comparisons of mean rank sums extended*. R package version 1.9.7. https://CRAN.R-project.org/package=PMCMRplus

Quintela-Sabarís, C., Mendes, L. A., & Domínguez, J. (2022). Vermicomposting as a sustainable option for managing biomass of the invasive tree Acacia dealbata link. *Sustainability*, *14*, 13828. https://doi.org/10.3390/su142113828

R Core Team (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rascio, N., & Navari-Izzo, F. (2011). Heavy metal hyperaccumulating plants: How and why do they do it? And what makes them so interesting? *Plant Science*, *180*, 169–181.

Reeves, R. D., Baker, A. J., Jaffré, T., et al. (2018). A global database for plants that hyperaccumulate metal and metalloid trace elements. *New Phytologist*, *218*, 407–411.

Sánchez-Hernández, J. C., & Domínguez, J. (2019). Dual role of vermicomposting in relation to environmental pollution: Detoxification and bioremediation. In J. C. Sánchez-Hernández (Ed.), *Bioremediation of agricultural soils* (pp. 217–230). CRC Press.

Simmonot, M.-O., Vaughan, J., & Laubie, B. (2018). Processing of bio-ore to products. In A. Van Der Ent, G. Echevarria, A. J. M. Baker, & J. L. Morel (Eds.), *Agromining: farming for metals* (pp. 39–51). Springer International Publishing.

Singh, J., & Kalamdhad, A. S. (2013). Reduction of bioavailability and leachability of heavy metals during vermicomposting of water hyacinth. *Environmental Science and Pollution Research*, *20*, 8974–8985.

Siqueira Freitas, D., Wurr Rodak, B., Rodrigues dos Reis, A., de Barros, R. F., Soares de Carvalho, T., Schulze, J., Carbone Carneiro, M. A., & Guimaraes Guilherme, L. R. (2018). Hidden nickel deficiency? Nickel fertilization via soil improves nitrogen metabolism and grain yield in soybean genotypes. *Frontiers in Plant Science*, *9*, 614. https://doi.org/10.3389/fpls.2018.00614

Srivastava, V., Goel, G., Thakur, V. K., Singh, R. P., Ferreira de Araujo, A. S., & Singh, P. (2020). Analysis and advanced characterization of municipal solid waste vermicompost maturity for a green environment. *Journal of Environmental Management*, *255*, 109914. https://doi.org/10.1016/j.jenvman.2019.109914

Swati, A., & Hait, S. (2017). Fate and bioavailability of heavy metals during vermicomposting of various organic wastes—A review. *Process Safety and Environmental Protection*, *109*, 30–45. https://doi.org/10.1016/j.psep.2017.03.031

Tan, X. W., Ikeda, H., & Oda, M. (2000). Effects of nickel concentration in the nutrient solution on the nitrogen assimilation and growth of tomato seedlings in hydroponic culture supplied with urea or nitrate as the sole nitrogen source. *Scientia Horticulturae*, *84*, 265–273. https://doi.org/10.1016/S0304-4238(99)00107-7

Tisserand, R., van Der Ent, A., Nkrumah, P. N., Sumail, S., & Echevarria, G. (2021). Improving tropical nickel agromining crop systems: The effects of chemical and organic fertilisation on nickel yield. *Plant and Soil*, *465*, 83–95.

van der Ent, A., Baker, A. J., Reeves, R. D., et al. (2013). Hyperaccumulators of metal and metalloid trace elements: Facts and fiction. *Plant and Soil*, *362*, 319–334.

van der Ent, A., Baker, A. J. M., Reeves, R. D., Chaney, R. L., Anderson, C. W., Meech, J. A., Erskine, P. D., Simonnot, M. O., Vaughan, J., Morel, J. L., Echevarria, G., Fogliani, B., Rongliang, Q., & Mulligan, D. R. (2015). Agromining: Farming for metals in the future? *Environmental Science & Technology*, *49*, 4773–4780.

van der Ent, A., Baker, A. J. M., Van Balgooy, M. M. J., & Tjoa, A. (2013). Ultramafic nickel laterites in Indonesia (Sulawesi, Halmahera): Mining, nickel hyperaccumulators and opportunities for phytomining. *Journal of Geochemical Exploration*, *128*, 72–79.

Wood, B. W., Reilly, C. C., & Nyczepir, A. P. (2006). Field deficiency of nickel in trees: Symptoms and causes. *Acta Horticulturae*, *721*, 83–98. https://doi.org/10.17660/ActaHortic.2006.721.10

How to cite this article: Quintela-Sabarís, C., Fernández Dosouto, A., Gómez-Brandón, M., & Domínguez, J. (2024). Can vermicomposting be used to process hyperaccumulator biomass in nickel agromining? *Ecological Research*, 1–10. https://doi.org/10.1111/1440-1703.12479