Applied Soil Ecology 97 (2016) 98–111

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Mapping earthworm communities in Europe

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ARTICLE INFO

Article history:
Received 20 March 2015
Received in revised form 14 August 2015
Accepted 21 August 2015
Available online 3 September 2015

Keywords:
Digital Soil Mapping
Earthworm community
EcoFINDERS
Soil Atlas
Soil biodiversity

ABSTRACT

Existing data sets on earthworm communities in Europe were collected, harmonized, collated, modelled and depicted on a soil biodiversity map. Digital Soil Mapping was applied using multiple regressions relating relatively low density earthworm community data to soil characteristics, land use, vegetation and climate factors (covariables) with a greater spatial resolution. Statistically significant relationships were used to build habitat–response models for maps depicting earthworm abundance and species diversity. While a good number of environmental predictors were significant in multiple regressions, geographical factors alone seem to be less relevant than climatic factors. Despite differing sampling protocols across the investigated European countries, land use and geological history were the most relevant factors determining the demography and diversity of the earthworms. Case studies from country-specific data sets (France, Germany, Ireland and The Netherlands) demonstrated the importance and efficiency of large databases for the detection of large spatial patterns that could be subsequently applied at smaller (local) scales.

1. Introduction

Monitoring soil biodiversity has been addressed by recent EU research programs (e.g. Bispo et al., 2009; Lemanceau, 2011) and national initiatives (e.g. RMQS and BiSQ: Gardi et al., 2009; Pulleman et al., 2012; Edaphobase: Burkhardt et al., 2014; and the UK Soil Indicators Consortium: Ritz et al., 2009). For instance, in the EU project EcoFINDERS a suite of indicators on soil biodiversity attributes, including microbia (bacteria and fungi), microfauna (protozoans and nematodes) and mesofauna (enchytraeids and microarthropods), was tested at 85 sites along a European transect (Stone et al., 2016). The aim was to demonstrate the feasibility of such an endeavour at a continental scale, and to collate the first set

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http://dx.doi.org/10.1016/j.apsoil.2015.08.015
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of harmonized earthworm data and maps and hence, allowing soil biodiversity to be upgraded from a theoretical to a practical issue on the environmental policy agenda at European and national levels.

A synthesis of existing data is not only timely, but also a more efficient use of limited resources for land management and decision making, than filling data gaps with additional costly surveys and monitoring. Such a database could also become a valuable source of information for awareness raising and environmental policy making, and possibly for some academic objectives, despite the fact that data were obtained from different countries, generated by different researchers using different sampling and identification methods, and with different project objectives.

Earthworms (Lumbricidae) are surprisingly under-recorded taxa (Carpenter et al., 2012) and were excluded from the aforementioned EcoFINDERS transect for practical and logistic reasons (Stone et al., 2016; B.S. Griffiths et al., *in progress*). However, macrofaunal groups are known to strongly reflect their habitats according to the niche modelling principles of Hutchinson (1957) and therefore, their geographical distribution can potentially be predicted from environmental data. For this reason, we collected and harmonized existing earthworm community data from several European countries and validated this information with environmental and climatic variables, generating the first continuous biodiversity map of earthworms.

The production of this first earthworm map faced a number of challenges:

1. The first challenge was to track and to source earthworm data, because there is no single public facility where such data can be accessed. Some progress has been achieved recently for different national data sets on soil biodiversity via the Global Biodiversity Information Facility (www.GBIF.org), the DRYAD Digital Repository (e.g., datadryad.org/resource/doi:10.5061/dryad.g7046), the Drilobase and Macrofauna database (earthworms.info and macrofauna.org) and the NBN Gateway (data.nbn.org.uk/Datasets). In addition, much of the earthworm data are often published in grey literature, such as project reports (e.g. Römbke et al., 2000, 2002; Schmidt et al., 2011; Rutgers and Dirven-Van Breemen, 2012 and references therein). Frequently, data are presented in appendices or dissertations and can only be accessed by contacting the source holders directly. We received data from earthworm inventories through personal contacts with professionals and researchers in different European countries, under the restriction to use the resulting database solely for producing these maps.
2. The second challenge was to compile sufficient relevant and reliable environmental information to enable meaningful analyses. We sought to link earthworm data to environmental variables in order to produce models for predicting their habitat–response relationships and hence, the distribution of earthworms according to independent niche modelling (*sensu* Hutchinson, 1957).
3. The third challenge was to harmonize the earthworm and environment variables as the collected information differed in relation to site selection, sampling design, collection, extraction, storage, the use of identification keys, and methods for soil analysis.

Belonging to the macrofauna, earthworms are among the few soil-dwelling organisms which are large enough to be seen by the naked eye. Earthworms are an important food source for small mammals (e.g. the mole: *Talpa europaea*) and birds (e.g. the black-tailed godwit *Limosa limosa)*. Importantly, fertile soils in temperate regions are greatly dependent on the dwelling/burrowing action of earthworms and for this reason they are considered important ecosystem engineers and used as valuable indicators for soil quality (Lavelle et al., 1997; Didden, 2003; Cluzeau et al., 2012; Van Groenigen et al., 2014). Although some earthworms are invasive species in northern America (e.g. Bohlen et al., 2004), in Europe Lumbricidae are native and charismatic for the general public, farmers and academics (Darwin, 1881).

Earthworms have been traditionally classified into three functional groups, representing different traits in the soil system (Bouché, 1977; Edwards and Bohlen, 1996), i.e. dwellers in the mineral layer (endogeics), dwellers in the litter layer (epigeics) and vertical burrowers (anecics). The abundance of earthworms is strongly affected by land use (Spurgeon et al., 2013). For example, the total abundance of earthworms in nutrient-rich grasslands under a temperate climate can easily differ one order of magnitude, as it has been reported to be as low as 138 individual m^{-2} (Sechi et al., 2015) and as high as 1333 individuals m^{-2} (Cluzeau et al., 2012). When taking into account all sites with recorded earthworms, the coefficient of variation of theirs abundance (individuals m^{-2}) at European level is high (134%) and, as expected, climate-related (a possible soil moisture deficit is known to reduce earthworm populations).

At a local scale, steep changes in the numerical abundance and diversity of earthworms can be expected at the interface between natural and agricultural land and at the edges between pastures and arable fields (Rutgers et al., 2009; Sechi et al., 2015). Consequently, digital soil mapping (DSM; McBratney et al., 2003) was utilized in the present study, building upon earlier efforts to map soil biodiversity in The Netherlands (Van Wijnen et al., 2012; Rutgers and Dirven-Van Breemen, 2012; Rutgers et al., 2012). DSM statistically correlates soil attributes with a low spatial resolution to attributes with a higher spatial resolution, such as the soil organic matter content and the land use type. In this study, earthworm community attributes (i.e. total abundance, abundance per taxon, Shannon diversity and richness) were used in a multiple regression analysis with data on soil characteristics, land use, vegetation and climate.

European maps of earthworm abundance (total and single species), richness and Shannon index were produced for areas where earthworm data were collected and subsequently harmonized, i.e. The Netherlands, Germany, Ireland, Northern Ireland, Scotland, France, Slovenia, Denmark, together with parts of Spain. The maps were created primarily to raise awareness, to advocate soil biodiversity as an environmental policy issue, and as a plea for enhancing long-term environmental monitoring, but not for analyzing earthworm community distributions in Europe. These maps and their associated raw data may enhance the recently launched *Global Soil Biodiversity Atlas* (www.globalsoilbiodiversity.org), a follow-up to the *European Atlas of Soil Biodiversity* (Jeffrey et al., 2010), and are open for future enrichment. To our knowledge no other continental scale soil biodiversity map has been generated using a DSM approach.

2. Materials and methods

2.1. Data collection and standardisation

Total abundance of earthworms and number of species or genera, adults and juveniles, together with selected biodiversity indices, were the targeted level of resolution for mapping. Thus, all potential contributors were asked to collect and assemble earthworm data on abundance (and/or biomass) per taxon (at species level, where possible), with an indication of the collection and identification method. The primary data providers, organized per country, are the authors of this article. The final database comprised earthworm records from 3838 sites in 8 countries

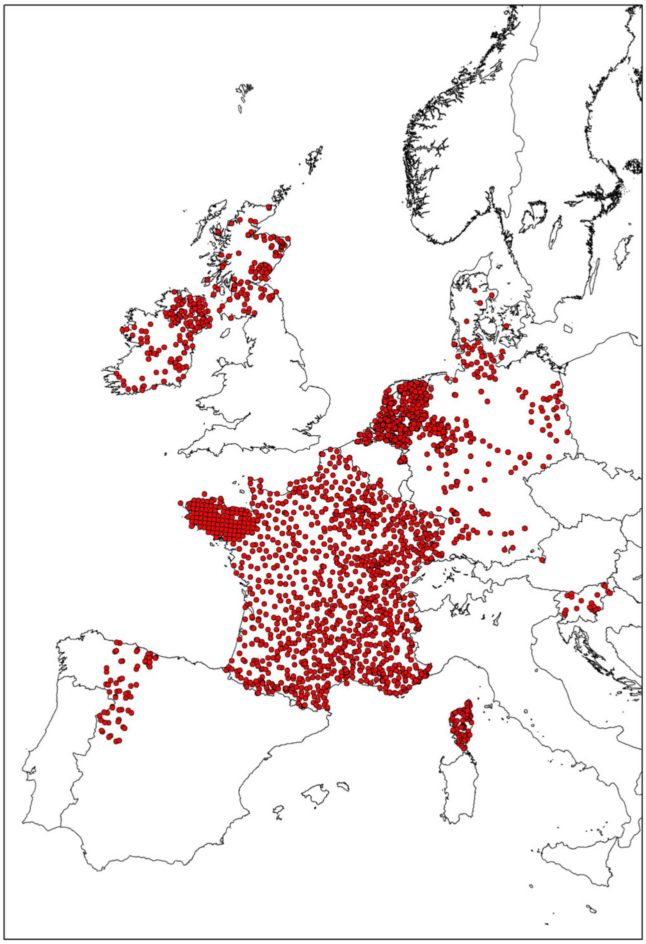

Fig. 1. Sites in Europe for which data on earthworm communities and habitat characteristics were collected, combined and harmonized into a single database. Geographical ranges span from 10°W to 30°E longitude and from 40°N to 59°N latitude.

(Fig. 1). Additionally we requested information on the sampling and corresponding environmental data, such as: geographical coordinates (WGS84, or any national coordinate system), land use or vegetation type, site selection and sampling method, date of sampling, soil acidity (pH with the indication of the method: in KCl, $CaCl_2$, or H_2O) and other soil properties such as soil organic matter content and the dominant mineral fractions (i.e. clay, silt, sand).

2.2. Soil texture and organic matter as potential predictors

In pedology and sedimentology soil granulometry as fraction(s) of mineral particles is usually reported without referring to soil organic matter. This is useful to identify the parent material, its origin and its geological history. However, from an ecological perspective, a more complete soil description which includes the mineral and the organic components will also provide a better picture of earthworms' preferred habitats. For example, in organic-rich soils (e.g. mires, fens and bogs) the proportion of mineral particles in relation to the total dry weight of the soil is very low. For this reason, we decided to enter these weighted percentages of soil texture and organic matter into the regressions, and corrected the GIS maps on soil texture according to these new potential predictors, i.e. silt, sand and clay fractions. JRC provided the soil properties (pH, SOM, texture, etc.) and the climate data for mapping, which included maximal, minimum and mean annual values for temperature and precipitation (see Jones et al., 2005).

2.3. Earthworm records and environment data per country

Sampling methods varied between and even within countries and included hand-sorting (in the field or in the laboratory) and the use (or not) of either mustard or formaldehyde solutions. Moreover, soil (composite) samples frequently differed in size between studies. Therefore, a summary of the methodologies for each of the 8 European countries is provided (Table 1) and described below in the following sequence: The Netherlands, Germany, Ireland, Northern Ireland (UK), Scotland (UK), France, Spain, Slovenia, and Denmark.

2.3.1. The Netherlands

Earthworm abundance data (per taxon, generally species) of 863 sites were collected from the database of the nationwide soil monitoring network (Rutgers et al., 2009; Mulder et al., 2011). Started in 1999, the monitoring network consists of approximately 360 sites in a random stratified design with 10 categories of land use and soil type representing about 75% of the terrestrial surface in The Netherlands. All sites were analyzed to get a suite of soil biodiversity indicators—the Biological Indicator of Soil Quality (BiSQ)—during at least two monitoring cycles. At each site, earthworms were extracted from 6 monoliths of $20 \times 20 \times 20$ cm through hand-sorting in the laboratory and identified to species level (Sims and Gerard, 1985). In addition, chemical and physical soil analyses were performed on all samples following standardized protocols in the soil monitoring network (Rutgers et al., 2008,

Table 1
Overview of the prevalent sampling methods for earthworm communities per country or project. The method section contains more details on sampling methods. Na = not applicable; – = not available or varying.

Country, project	Method HS = hand-sorting F = formaldehyde M = mustard	Number of applications and concentrations (formaldehyde or mustard solution)	Surface per sub-sample (m^2)	Soil volume hand-sorting per subsample (L)	Number of sub-samples
NETH	HS	Na	0.04	8	6
GER[a]	HS, F or both	–	–	–	–
FRA Bouché	HS	–	0.3	300	–
FRA RMQS[b]	F + HS	3×10 L (0.25–0.4%)	1.0(F); 0.063(HS)	16	3–6
FRA AgrInnov	HS	Na	0.04	8	6
IRE	HS (+M/F)	2×2.5 L (0.01%)	0.063	16	4
N-IRE	F	2×5 L (0.4%)	0.25	Na	10
SCOT	F	2×4.5 L (0.5%)	0.25	Na	5
SLO	HS (+F)	$2 \times$ (0.2–0.4%)	0.25–5	24.5–125	3–10
SPA	F + HS	1×2.5 L (0.55%)	0.5	100	2
DEN	HS	Na	0.063–0.25	19–75	–

[a] The data from Germany were composed from many projects.
[b] FRA-RMQS includes methods from RMQS-BioDIv, BIOindicateursII and VitiEcoBioSol project (see Section 2).

2009). The sites in the network are represented at the dimension of farms, typically 5–50 ha, or less in the case of natural areas (Rutgers et al., 2008; Cohen and Mulder, 2014). The earthworm data from this data set are also accessible via the Global Biodiversity Information Facility (www.GBIF.org).

2.3.2. Germany

Earthworm data were extracted from the Edaphobase portal (http://portal.edaphobase.org; Burkhardt et al., 2014). This database contains data from museum collections, published literature, grey literature such as research reports and master theses as well as permanent soil monitoring data from some federal states. Hence, the set is heterogeneous regarding data gaps and methods used. We only considered those data that fulfilled the following requirements: the sampling campaigns had to be suitable to assess quantitatively the composition of the entire earthworm community (i.e. no museum specimens; earthworms collected by hand-sorting, or extracted by formaldehyde or mustard solution; Jänsch et al., 2013), and geographical reference data (coordinates) had to be available as well as physico-chemical characteristics for at least pH, texture and organic carbon content. Furthermore, records from sites with anthropogenic impact other than physical soil cultivation measures (e.g., heavy metals, pollution, pesticide application, excessive nitrogen deposition) were not included. Data derived from electrical (octet) extraction methods were disregarded as this method is known to underestimate earthworms' abundance and diversity. Finally data of 712 sites fulfilled these requirements.

2.3.3. Ireland

Earthworm data of 144 sites for the Republic of Ireland were collated from a national soil biodiversity survey (Keith et al., 2012), published papers (Little and Bolger, 1995; Schmidt and Curry, 2001) and PhD theses (Roarty, 2010; Artuso, 2011). The soil biodiversity survey (CréBeo Soil Biodiversity Project; Schmidt et al., 2011) sampled earthworms across 61 sites in 2006 and 2007. These sites were selected from the National Soils Database (NSD; Fay et al., 2007) and included arable, pasture, rough grazing, forest and bog land. A 20 × 20 m plot was centered on the NSD GPS coordinates of each site and the earthworms were extracted by hand-sorting four 25 × 25 × 25 cm soil blocks and, where feasible, by chemical expellant (mostly mustard oil solution containing isothiocyanate) from four additional 50 × 50 cm quadrats. Total fresh earthworm biomass was recorded and worms were then preserved in 4% formaldehyde solution. Mature and sub-adult individuals were identified to species level using the key of Sims and Gerard (1985) and juveniles were separated into pigmented tanylobic, pigmented epilobic and unpigmented earthworms. Soil pH (H_2O), organic matter and texture variables were derived from the NSD. Earthworms were extracted by hand-sorting in arable and grassland habitats (Schmidt and Curry, 2001; Roarty, 2010; Artuso, 2011) or extracted by mustard solution in grass and forest habitats (Little and Bolger, 1995); soil variables were taken from these publications.

2.3.4. Northern Ireland

Earthworm data of 157 sites were collected within the framework of monitoring *Arthurdendyus triangulatus* distribution in agricultural grasslands (Murchie et al., 2003), an invasive terrestrial flatworm that predates earthworms (Blackshaw and Stewart, 1992; Murchie and Gordon, 2013). The initial survey was conducted from January to May 1991. Seventy five grassland fields were randomly selected from a geographically-stratified sampling of farms throughout Ulster (Farm Census Office, Dundonald House, Belfast, Northern Ireland). Follow-up surveys of 31 and 52 of the original 75 fields were done from April to May 1998 and 1999, respectively. Within each field, ten metal quadrats (50 × 50 cm) were arranged in a V or W formation. The quadrats were introduced 3 cm into the ground at 10 m intervals. Two applications of 5 L of 0.4% formaldehyde solution, 15 min apart, were applied to each quadrat and the expelled earthworms (and flatworms) preserved in 5% formaldehyde solution. Adults were identified to species using the key of Sims and Gerard (1985) and the juveniles were identified to genera. Field history such as grazing and fertilizer-input were recorded on site by interviewing the farmer. For the surveys in 1991 and 1999, soil samples were air-dried and sieved (<2 mm) prior to standard soil pH determination in a 1:2.5 soil:water ratio. Additional information about soil characteristics (soil-type, land cover, climate and topography) was derived from the Northern Ireland Soil Survey (Cruickshank, 1997; Jordan et al., 1997).

2.3.5. Scotland

Earthworm data of 235 sites were collected using a stratified random sampling from 100 arable farms throughout Scotland, which were selected from the national agricultural census (Scottish Government) during 1991 and 1992 (Boag et al., 1997). Wherever possible earthworms were extracted from one arable and one permanent pasture fields. However, only 56 farms had both field types and, of the remainder, 38 farms had only permanent pasture fields and six farms comprised only arable fields. In a randomly selected area at each selected field, five 50 × 50 cm metal quadrats were introduced 5–10 cm into the ground at 10 m intervals in a polygonal array. If present, vegetation was cut to ground level and removed prior to two applications of 4.5 L of 0.5% formaldehyde solution (Raw, 1959). All earthworms which emerged were collected and preserved in 4% formaldehyde solution for subsequent counting and identification at a later date. Samples were transported from the field to the laboratory within 10 h. Earthworms were identified using their external characteristics (Sims and Gerard, 1985) and by comparing them with type specimens obtained from the Natural History Museum, London. The biomass of all individual earthworms collected was also determined. Additionally, from each field, a soil sample was taken for soil analyses which comprised of 20 sub-samples collected using a trowel from a depth of 5-–15 cm.

2.3.6. France

Earthworm data (abundance per taxon at the subspecies level) were extracted from 1423 locations, included in the two databases ECORDRE (Soto and Bouché, 1993) and EcoBiosoil (Cluzeau et al., 2010). From the ECORDRE database, the Bouché's data set corresponds to 1157 sites sampled throughout France (55% of agricultural areas, 40% of forest and semi-natural areas; 5% of gardens and verges). Sampling was performed from 1963 to 1969; at each site, earthworms were sampled by excavating soil blocks of 100 × 100 × 30 cm. Environmental data of the sampled sites, including location, vegetation cover and soil chemical properties, were collected as well (Bouché, 1972).

From the EcoBiosoil database, 4 data sets were used:

i) the RMQS BioDiv's data set (Cluzeau et al., 2012) representing 109 sites located in the Brittany region (West of France): land uses here were mainly meadows and arable soils (90%) and a few consisted of natural areas. Sampling campaigns were performed in 2006 and 2007 based on a systematic frame (16 × 16 km). Earthworms were extracted using formaldehyde solution coupled with a hand-sorting method (Bouché, 1977; Cluzeau et al., 1999), i.e. three applications of 10 L (formaldehyde solutions: twice 0.25% and once 0.4%) were applied to 1 m^2 at 15 min intervals. Afterwards, the remaining earthworms were collected by hand-sorting from a 25 × 25 × 25 cm soil block in the central m^2 for further correction.

ii) the BIOindicateursII's data set (Pérès et al., 2011,http://ecobiosoil.univ-rennes1.fr/ADEME-Bioindicateur/english/index.php) corresponded to 13 sites (arable 42%, pasture 13%, woodland-wasteland 34%, forest 11%) sampled between 2009 and 2011 through France, resulting in 47 contrasted plots. In each plot, four soil samples were collected and processed following the same methods as for the RMQS BioDiv data set.

iii) the VitiEcoBioSol's data set consisted of 18 monitoring sites in Champagne vineyards (http://www.gessol.fr/living-soil-champagne-vineyards-vitiecobiosol); sites were sampled from 1985 up to 2010 (several times per site) using the same method as described for the RMQS BioDiv data set.

iv) the AgrInnov's data set (http://www.ofsv.org/index.php/agrinnov) consisting of 89 sites (crops and vineyards); sampling was done during 2013 and 2014; at each site, earthworms were hand-sorted from 6 soil blocks (20 × 20 × 20 cm).

For all data sets, taxonomical identification of the specimens collected was achieved in the laboratory according to Bouché (1972). For all sites, soil chemical analyses were performed by the official soil laboratory of Arras (France) using standardized protocols.

2.3.7. Spain

Earthworm data (abundance at the species level and biomass) were collected from 63 localities belonging to four provinces in NW Spain (Asturias, León, Zamora and Salamanca; Briones et al., 1991, 1992). At each locality three different habitats (pastures, riverbanks and wooded areas) were sampled, giving a total number of 189 locations surveyed over two years (1987 and 1988). On every sampling occasion two rectangular areas (50 × 100 cm separated by 1 m) were cleared from vegetation and litter (which was carefully checked for earthworms) and 2.5 L of 0.55% formaldehyde solution was applied to the surface. The earthworms emerging from the soil were picked using tweezers and rapidly transferred to clean water. After 30 min the two areas were excavated down to 20 cm and the earthworms were hand-sorted. Abundance data was then referred to 1 m^2 area, counting the two rectangular blocks together. All earthworms collected were fixed in a 1:1 solution of 96% ethanol and 10% formaldehyde solution prior to being preserved in 10% formaldehyde solution. Taxonomic identification of the collected specimens was achieved by following Omodeo (1956), Álvarez (1966) and Bouché (1972). After identification of all preserved specimens (adults and juveniles), their biomass was also recorded. In addition, at every location, one composite soil sample was taken from the top 20 cm of the soil profile and homogenised, air dried and sieved (<2 mm) for further chemical characterisation. Soil pH was measured in distilled water (1:2.5 w/v) according to Guitián and Carballas (1976). Total carbon content was estimated following the standard protocol (MAPA, 1982) and soil texture was determined by the pipette method.

2.3.8. Slovenia

Earthworm data from 89 locations were gathered from unpublished graduation theses defended at the Biotechnical Faculty of the University of Ljubljana (1993–2006), from national ARRS-CRP-V4-1083 (2012–2013) and ARRS-J4-4224 (2011–2014) projects, and from the EcoFINDERS project (2011–2014). Until 2006, earthworms were sampled in the field by hand-sorting of an area of 50 × 50 cm to the bottom of the soil profile (or max. 50 cm), 10 subsamples were put together for one composite sample per sampling location or hand-sorting of an area of 250 × 200 cm to the bottom of the soil profile. After 2011, a combination of hand-sorting and formaldehyde extraction has been used (ISO 23,611-1), with 3 subsamples per location: the excavated volume was either 50 × 50 × 50 cm or 35 × 35 × 20 cm with successive formaldehyde applications afterwards (twice 0.2% and once 0.4%). Earthworm identification was based on the keys by Mršić (1991). In addition, at each sampling location, some descriptive environmental parameters (soil type, land use, and vegetation) were also recorded. The Slovenian soil map at the scale 1:25000 was used for assigning more detailed soil properties (pH, organic matter content, texture) to those localities where this information was missing (TIS, 2015).

2.3.9. Denmark

The earthworm data set from 78 sites in Denmark was obtained on the basis of soil blocks varying in size from 25 × 25 cm to 50 × 50 cm to a depth of 30 cm. They originated from several Aarhus University research projects, which were performed in agricultural lands, except the most Eastern location in Jutland (Djursland) which was a permanent grassland. The soil blocks were carefully excavated and transported to the laboratory and earthworms were identified to species according to Sims and Gerard (1985). Fresh weight was determined after keeping earthworms overnight in Petri-dishes with wet filter paper to empty their guts. Soil properties were determined according to the Danish manual on soil physico-chemical analyses (Sørensen and Bülow-Olsen, 1994). The identification of *Lumbricus herculeus* (Savigny) was confirmed by barcoding of COI (James et al., 2010).

2.4. Harmonization, depuration, exclusion and imputation of earthworm data

Several attributes of earthworm communities were selected as end points for the multiple regression modelling: total abundance (number m^{-2}), abundance per taxon (generally species; number m^{-2}), richness (number of taxa), and a biodiversity index (Shannon–Wiener). It was not possible to derive regression models at European level for the three functional groups (endogeic, epigeic and anecic earthworms) because we did not possess large-scale trait identification keys for the majority of the 168 unique species in the database. Additionally, in most sets, some earthworms could not be identified to species or even to genus level; therefore, these observations were listed as either 'unidentified' or 'juveniles'. If no other taxon was present in the sample, the number of taxa was set to 1; in all other cases the number of taxa was equal to the number of identified taxa. Identification levels for earthworms differed per data set. For instance, the higher taxonomical resolution in the original ECORDRE data set, reflecting many subspecies of earthworms described and recorded for France, forced us to lump the records at a lower resolution (higher taxonomical scale, i.e., only at species level). After this adjustment, the coefficient of variation for biodiversity of the French data set (51.1%) became comparable to the Dutch and German data sets (55.0% and 58.8%, respectively).

2.5. Harmonization, depuration, exclusion and imputation of environment data

Several environmental factors as potential predictors for earthworm community attributes were selected when satisfying two requirements: (1) availability of continuous EU maps with a reasonable resolution for the selected predictor, and (2) a mechanistic model for plausible explanation of the relationship. Potential environmental predictors included: coordinates and elevation (WGS84), climate factors (minimum, maximum and average annual temperature; minimum, maximum and average annual precipitation), soil texture (% sand, % silt, % clay), soil organic matter (%), soil–pH(H_2O), land use and vegetation *sensu* CORINE land cover system (www.eea.europa.eu). Sampling date was omitted because of large data gaps, although it is known that it affects the estimates of soil invertebrate abundances (Mulder et al., 2003).

A complete set of environmental data for each potential predictor was required for multiple regression modeling, linking empirical observations on earthworm communities to potential environmental predictors. Some earthworm records were not accompanied with a complete set of environmental predictors, and they had to be estimated from other sources, e.g. national soil maps. Mismatches and missing data were detected and corrected using spatial explicit data sets (e.g. Jones et al., 2005).

2.6. Habitat response modelling

Generalized Linear Regression (GLM) models of the Gaussian family (McCullagh and Nelder, 1989) were used to relate earthworm community attributes (EWca: total abundance, total number of observed taxa, Shannon Index) to potential environmental predictors for which high resolution European maps were available.

The models to be calibrated were all formulated according to the following syntax (Eq. (1); Table 2 provides predictor codes and some statistics):

$$\begin{aligned}\mathrm{EWca} = {} & \mathrm{intercept} + a \times [\mathrm{Agr}] + b \times [\mathrm{Cro}] + c \times [\mathrm{Orc}] + d \times [\mathrm{Vin}] + e \times [\mathrm{For}] + f \times [\mathrm{Ngr}] + g \times [\mathrm{Hea}] + h \times [\mathrm{Par}] + i \times [\mathrm{long}] + j \times [\mathrm{long}]^2 \\ & + k \times [\mathrm{lat}] + l \times [\mathrm{lat}]^2 + m \times [\mathrm{ele}] + n \times [\mathrm{ele}]^2 + o \times [\mathrm{pH}] + p \times [\mathrm{pH}]^2 + q \times [\mathrm{som}] + r \times [\mathrm{som}]^2 + s \times [\mathrm{cla}] + t \times [\mathrm{cla}]^2 + u \times [\mathrm{sil}] \\ & + v \times [\mathrm{sil}]^2 + w \times [\mathrm{san}] + x \times [\mathrm{san}]^2 + y \times [\mathrm{premin}] + z \times [\mathrm{premin}]^2 + aa \times [\mathrm{premax}] + ab \times [\mathrm{premax}]^2 + ac \times [\mathrm{preave}] + ad \\ & \times [\mathrm{preave}]^2 + ae \times [\mathrm{tempmin}] + af \times [\mathrm{tempmin}]^2 + ag \times [\mathrm{tempmax}] + ah \times [\mathrm{tempmax}]^2 + ai \times [\mathrm{tempave}] + aj \times [\mathrm{tempave}]^2 \end{aligned} \tag{1}$$

The quadratic terms for the scalar predictors in the regression formula allow for predicting non-linear response behaviours which can be ascribed to either maxima (optima) or minima (stress) conditions. In this way, these formulae relate the numerical abundance of each taxon to the environmental predictors, while ignoring cross-products. The regression models were then calibrated using a stepwise procedure based on the Bayesian Information Criterion (BIC; Schwarz, 1978). This was done in order to restrict the addition of terms to those that had a significant ($p < 0.05$) contribution to the overall model. The main goal was to describe patterns by reducing false negatives (any empirical record not predicted by the model) with overfitting. The higher the number of polynomials, the greater the likelihood that the resulting model will overfit the collected empirical data (Araújo and Guisan, 2006). Calculations were conducted using S-Plus 2000 (MathSoft, Cambridge, MA). Subsequently, the calibrated regression formulae were used to generate continuous maps of earthworm community attributes by substituting continuously mapped values for the model predictors in the calibrated regression formulae.

Regressions were performed on the collated database with earthworm data from 8 countries (Fig. 1) in order to avoid contiguous effects at the borders of the countries. However, this resulted in some loss of reliability of the model when predicting earthworm abundance and species composition for those countries with scarce observations. Consequently, we decided to perform regressions on subsets of the database for a few countries to show possible artifacts. This was done for The Netherlands, Germany, France, and Ireland including Northern Ireland. These national maps are available in the online Appendix A (Supplementary electronic material Fig. S1 Fig. S1 and S2).

Some areas, land uses, soil and vegetation types were excluded from the maps, due to lack of data. Notwithstanding the incomplete country data, we applied selection criteria which resulted in data from certain habitats, such as mountainous areas (>1500 m a.s.l.), sand dunes, surface and riverine water systems, urban and industrial areas (factories, roads, railways, and greenhouses), peat bogs and swamps to be excluded from the analyses and maps.

Table 2
Abbreviations and names of predictors used in the regression analysis of the European data set on earthworm communities. For the categorical predictors (Boolean-type) the total sum is provided summarizing the total data set with 3838 records. For the continuous predictors three percentiles (0.05, 0.5 and 0.95) of the final data set are provided.

Abbr.	Predictor name	Units	Sum	Percentiles		
				0.05	0.5	0.95
Agr	Agricultural grass	Boolean	1395			
Cro	Arable crop	Boolean	796			
Orc	Orchards	Boolean	41			
Vin	Vineyards	Boolean	102			
For	(Mixed) forest, all types	Boolean	610			
Hea	Heather, shrubs and moors	Boolean	99			
Ngr	Semi-natural grassland	Boolean	753			
Par	Parks, gardens, verges, urban green areas	Boolean	34			
Long	Longitude	WGS84 decimal system		−6.7	5.0	12.6
Lat	Latitude	WGS84 decimal system		42.4	49.5	55.9
Ele	Elevation	m (a.s.l.)		−2.2	110	901
pH	Soil pH–H_2O	pH units		4.3	6.2	8.0
Som	Soil organic matter	% dry matter		1.4	4.8	22
Cla	Clay particles	% dry matter		1.8	13.5	43
Sil	Silt particles	% dry matter		4.6	24	58
San	Sand particles	% dry matter		8.5	49	89
Premin	Average minimal precipitation	$\mathrm{cm\,yr^{-1}}$		18	47	70
Premax	Average maximal precipitation	$\mathrm{cm\,yr^{-1}}$		64	84	132
Preave	Average annual precipitation	$\mathrm{cm\,yr^{-1}}$		47	66	101
Tempmin	Average minimum temperature	°C		−1.7	2.0	6.0
Tempmax	Average maximum temperature	°C		14.1	17.1	21.5
Tempave	Average annual temperature	°C		7.2	9.5	12.9

3. Results and discussion

3.1. Building a harmonized database for earthworm records in Europe

After discarding records with incomplete or unreliable data, sometimes leading to the elimination of data sets of entire countries, we were able to assemble an earthworm database with abundance and species composition and associated environmental characteristics from 3838 sites in 8 countries (minimum 71 sites, maximum 1423 sites per country: Fig. 1, Table 3). The Netherlands had the highest data density (2.1 observations per 100 km^2) and the largest European country, France, had the highest number of records but a lower data density (with 1423 observations per 547,030 km^2, i.e. a data density of 0.26 per 100 km^2: Table 3).

Methods for sampling earthworm communities differed per country (Table 1) and even within countries methods can differ per project. We only considered data from sampling methods using (mechanical) hand-sorting and/or application of chemical expellant (formaldehyde or mustard). However, considerable differences exist between the choice for the chemical expellant, the concentrations of formaldehyde, the number of additions, the surfaces, the volumes excavated for hand-sorting, and the subsamples used for one composite sample. It was impossible to account for all these differences, and although they were sometimes small, this issue greatly increased the total variation associated with the collated data sets (cf. Bartlett et al., 2010) and requires more harmonization in earthworm soil monitoring to minimize variation in the future.

Another source of variation came from application of a small number of defined land use types (CORINE). However, the management within a defined land use type may significantly differ over regions and countries: examples are orchards and conventionally-managed ‘semi-natural’ grasslands. Furthermore, due to missing data we were unable to separate plantations from natural forests (Table 3). These sources of variation by wrong or limited assignments to land use types were accepted in this study, because land use is known to strongly affect earthworms (Lavelle et al., 1997; Spurgeon et al., 2013).

Although we had to assume that the taxonomical identification was correct (the Pearson’s correlation coefficients between species were in nearly all cases weakly positive; with negative correlations there is a small chance that the two species involved are actually two populations belonging to one single species), the sum of all unidentified individuals showed negative correlations with the most abundant earthworm species recorded (i.e. *Aporrectodea caliginosa*; see online Appendix A Fig. S3). Hence, we cannot preclude that some identifications were incorrect or at least that synonyms have been used resulting from different identification keys or the existing knowledge at the time of the sampling. In many data sets, unidentified individuals were given as ‘unknowns’. This frequently referred to juveniles, which are more difficult or even impossible to identify (e.g. *Lumbricus* juveniles). Some individuals were identified only to genus level, e.g. in the German and Dutch data sets.

Two important issues concerning earthworm community data collection come from theoretical ecology. Firstly, if we assume that earthworm communities gradually change along one or more environmental gradients (the continuum model), their distribution should be monotonic and curvilinear, i.e. Gaussian (Gauch and Whittaker, 1972). However, habitat–responses of the majority of plants and invertebrates are rarely Gaussian (e.g., Austin, 1980; Mulder et al., 2003, respectively). Still, Gaussian structures represent convenient starting points, because they allow the identification of optimum and minimum ranges through bell-shaped curves.

The second important issue was the inclusion of records where earthworms were absent. For example, due to the different sampling design of monoliths in The Netherlands, nearly 12% of the

Table 3
Metadata of record collections used for mapping earthworm communities in Europe. Two smaller data sets were combined to cover the entire island of Ireland. Agr: agricultural grassland, Cro: crop, Orc: orchards, Vin: vineyards, For: forest (all types), Ngr: (semi) natural grassland, Hea: heathland, moors, shrubs, Par: Parks, gardens, verges, urban green areas.

Country	Total records, (#/100 km^2)	Agr	Number of sites per land use, vegetation type						Par	Average temperature at all sites (°C)	Average precipitation at all sites (cm/yr)	Average abundance (n/m^2) (0.05–0.95 percentiles)	Total number and mean taxa (0.05–0.95 percentiles), zero’s	Shannon–Wiener (H′) diversity index (adimensional) ± stand. dev.
			Cro	Orc	Vin	For	Ngr	Hea						
NETH	863 (2.1)	494	246	16	0	30	35	28	14	9.3	65	252 (0–725)	37 3.5 (0–7) 90	0.91 ± 0.49
GER	712 (0.20)	60	257	0	0	159	234	0	2	8.7	65	114 (4–478)	31 4.3 (1–8) 3	0.89 ± 0.52
FRA	1423 (0.26)	691	111	25	80	298	129	63	18	10.8	68	61 (3–258)	109 4.5 (1–9) 12	1.18 ± 0.51
IRE + N-IRE	301 (0.32)	8	43	0	0	25	217	8	0	8.9	87	164 (0–574)	24 6.0 (0–10) 19	1.15 ± 0.43
SCOT	200 (0.25)	132	68	0	0	0	0	0	0	7.9	83	37 (0–111)	15 3.7 (0–7) 15	0.97 ± 0.48
SLO	71 (0.35)	0	2	0	22	35	12	0	0	9.1	98	16 (0–57)	40 2.8 (0–7) 12	0.73 ± 0.56
SPA	189 (0.04)	0	0	0	0	63	126	0	0	11.9	51	73 (3–227)	35 4.9 (1–9) 1	1.06 ± 0.49
DEN	79 (0.18)	10	69	0	0	0	0	0	0	7.6	58	136 (11–340)	11 3.2 (1–7) 4	0.85 ± 0.50

total number of observations was zero, whereas in the case of Germany and France this number was much lower (<1%). For accurate mapping of the distribution of earthworm communities in different habitats zero observations (no earthworms) were considered to be equally valuable as positive observations (Table 3). Taxa and Shannon index were calculated only for those records where at least one individual was recorded.

3.2. Multiple regression models

Several attributes of earthworm communities were analysed with multiple regressions which yielded a set of significant Gaussian models. Variance inflation factors (VIF) were calculated and interpreted according to Kline (1998) and O'Brian (2007). The generated VIF values indicated that predictors' co-linearities were unlikely (VIF < 10). The Gaussian models (Eqs. (2)–(4) inferred at European level from the total database (abun = total abundance; taxa = species richness; shan = Shannon–Wiener index, see Table 2 for a glossary of the predictors used) were:

$$\mathrm{Abun} = -4710 + 151 \times \mathrm{lat} - 1.49 \times \mathrm{lat}^2 + 117 \times \mathrm{pH} - 8.03 \times \mathrm{pH}^2 + 11.8 \times \mathrm{som} - 0.167 \times \mathrm{som}^2 - 1.03 \times \mathrm{san} + 2801 \times \mathrm{Agr} - 43.9 \times \mathrm{For} - 89.9 \times \mathrm{Hea} - 0.151 \times \mathrm{ele} + 7.17 \times 10^{-5} \times \mathrm{ele}^2 + 99.8 \times \mathrm{tempmax} - 3.09 \times \mathrm{tempmax}^2 - 10.2 \times \mathrm{premin} + 0.0593 \times \mathrm{premin}^2 - 0.0117 \times \mathrm{premax}^2 + 4.46 \times \mathrm{preve}\ (\text{coefficient of determination } R^2 = 25.2\%) \tag{2}$$

$$\mathrm{Taxa} = 9.48 - 9.27 \times 10^{-4} \times \mathrm{lat}^2 - 0.0492 \times \mathrm{long} - 4.73 \times 10^{-4} \times \mathrm{som}^2 + 0.0390 \times \mathrm{san} - 5.80 \times 10^{-4} \times \mathrm{san}^2 - 0.581 \times \mathrm{Agr} - 1.92 \times \mathrm{Cro} - 2.75 \times \mathrm{vin} - 1.66 \times \mathrm{For} - 1.86 \times \mathrm{Hea} - 7.98 \times 10^{-7} \times \mathrm{ele}^2 - 6.37 \times 10^{-3} \times \mathrm{tempmax}^2 + 5.56 \times 10^{-3} \times \mathrm{premin}\ (\text{coefficient of determination } R^2 = 24.9\%) \tag{3}$$

$$\mathrm{Shan} = -1.54 - 1.5 \times 10^{-4} \times 10^{-4} \times \mathrm{lat}^2 - 1.27 \times 10^{-3} \times \mathrm{long}^2 + 0.907 \times \mathrm{pH} - 0.0708 \times \mathrm{pH}^2 + 0.0102 \times \mathrm{san} - 1.31 \times 10^{-4} \times \mathrm{san}^2 - 0.380 \times \mathrm{Cro} - 0.564 \times \mathrm{vin} - 0.163 \times \mathrm{For} - 0.386 \times \mathrm{Hea} - 1.22 \times 10^{-7} \times \mathrm{ele}^2 + 4.80 \times 10^{-3} \times \mathrm{premin}\ (\text{coefficient of determination } R^2 = 26.66\%) \tag{4}$$

This exercise delivered models for earthworms from data of several European countries, which linked earthworm community parameters to the selection of environmental predictors of Eq. (1). Potential predictors demonstrated multicollinearity, as in the case of most climatic parameters (although the minimal rainfall, which can be seen as a humidity proxy, occurred in all three models, as expected for earthworms), and some predictors (expected to be significant) were almost "invisible" in the model outputs (*sensu* Mac Nally, 2002). Furthermore, the scale of this exercise was so big, that much smaller local trends remained undetected due to overfitting. Although the collected data sets had different weight (sample numbers) and quality (data resolution), the harmonized database was suitable for regression analyses. However, further improvements remain possible, e.g. compliance between methods, inclusion of sampling date, and site selection should be consistent or accounted for to improve the usefulness of future databases. Moreover, other statistical techniques than the classical multiple linear regressions might be more appropriate for such data sets and digital soil mapping, like non-parametric inference with random-forests or boosted regression trees.

3.3. Data quality, density and maps

Any climate and habitat characteristic related to earthworm distribution (Eq. (1)) can be used for this modelling (Eqs. (2)–(4)) and mapping initiative (Figs. 2–4). However, only characteristics for which high resolution maps were available are applicable, otherwise maps could not be inferred using these Gaussian models. For instance, it is known that earthworms are sensitive to tillage (Pelosi et al., 2014; Crittenden et al., 2015), but this information was unavailable at European scale. Therefore, availability of tillage-related data with all associated data corresponding to the earthworm records is in fact a prerequisite for a possible improvement.

There were no data sets in which earthworms were gathered using identical methodologies. In fact, all collected parameters varied across sites: sampling designs (stratified, random, point or area representation, zero's, subsampling and combining samples), sizes (representative surface, single or multiple monoliths), extraction (applications of formaldehyde solution, hand-sorting in the field or at the laboratory or a combination of all these) and identification methods. Many earthworm records had to be discarded because there was no available information on soil texture, vegetation type or soil characteristics, which are essential for predicting earthworm distributions. Indeed, we had to decide whether to include a potential predictor, and discard many observations without these data, or to discard the potential predictor from the regressions such as sampling date. It is known that earthworm abundance is mainly greater during late spring, or early autumn, but not in winter (even if it is variable depending on region and land use). In the German data set, information on the sampling date was often missing, and this predictor had to be discarded. However, we concluded that by discarding sampling date, the explained deviance would decrease, but without seriously affecting the resulting maps shown here.

We have predicted earthworm distributions in those areas for which earthworm data were collected in the database, plus some additional areas to produce continuous maps, i.e. England, Belgium, Luxembourg, Austria and the north of Spain (Figs. 2–4). These areas were surrounded by data dense countries, with

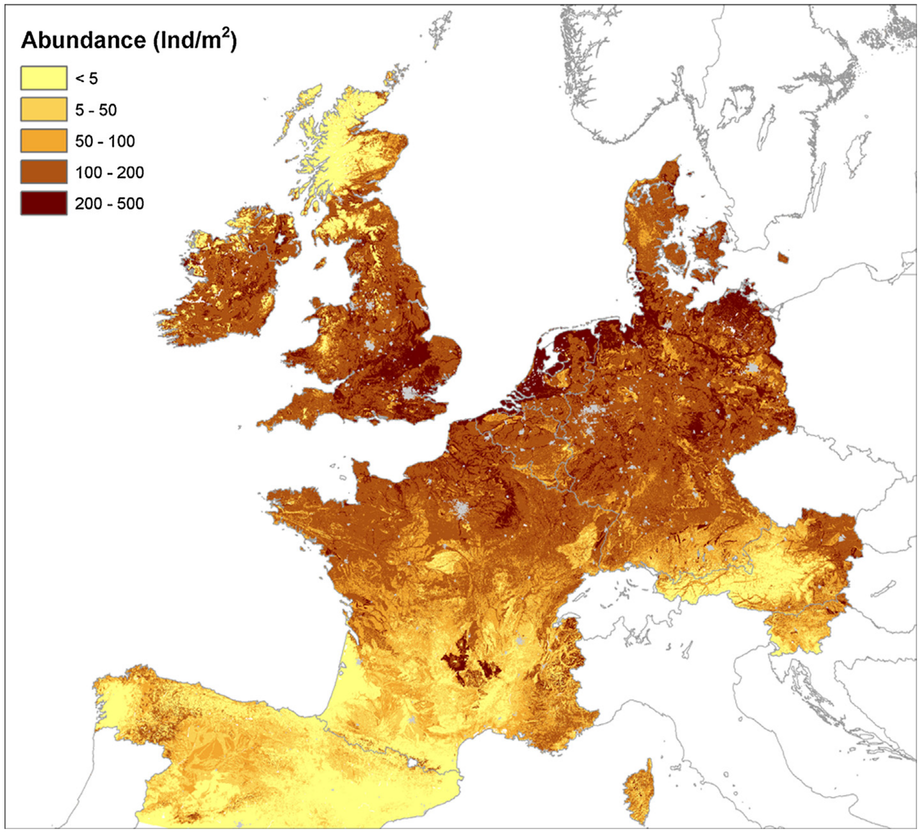

Fig. 2. Predicted abundance of earthworms in Europe. The predictions were derived from regression models and plotted on high-resolution maps for the habitat characteristics. The regressions models obtained from the earthworm data of the sites in Fig. 1 were provided and discussed in the text.

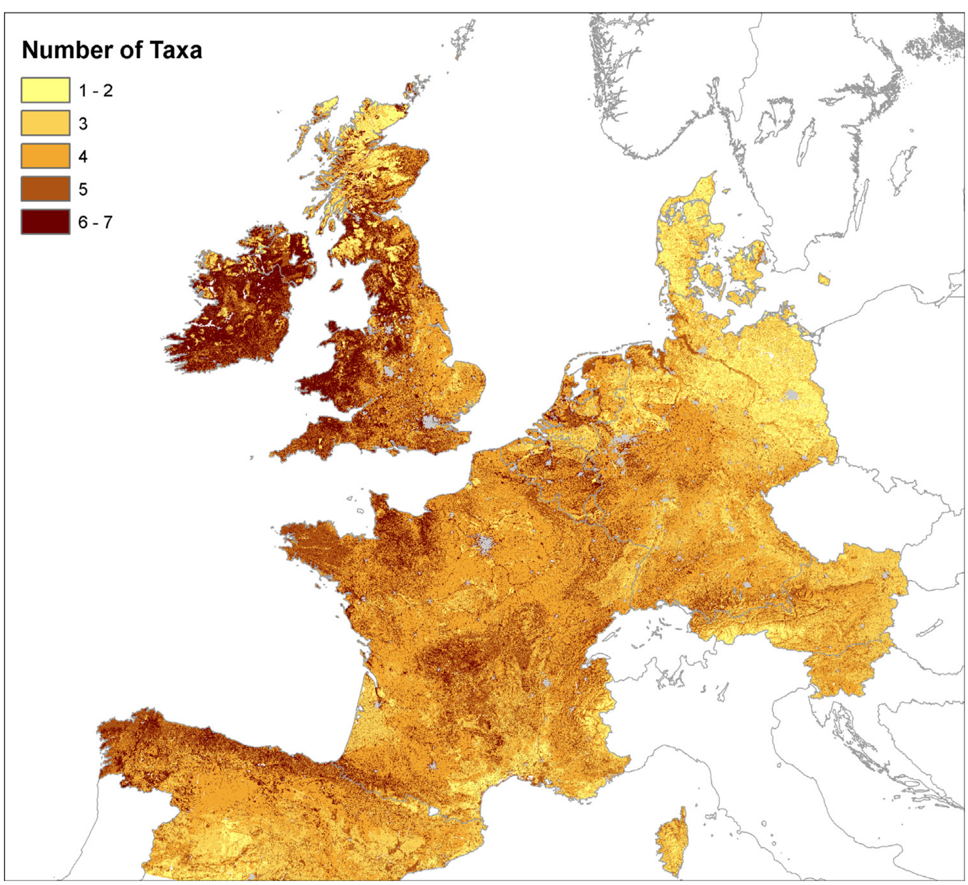

Fig. 3. Predicted richness of earthworm communities in Europe. Please compare with Fig. 2 to see the different (Atlantic versus North Sea-driven) influences on the targeted earthworms.

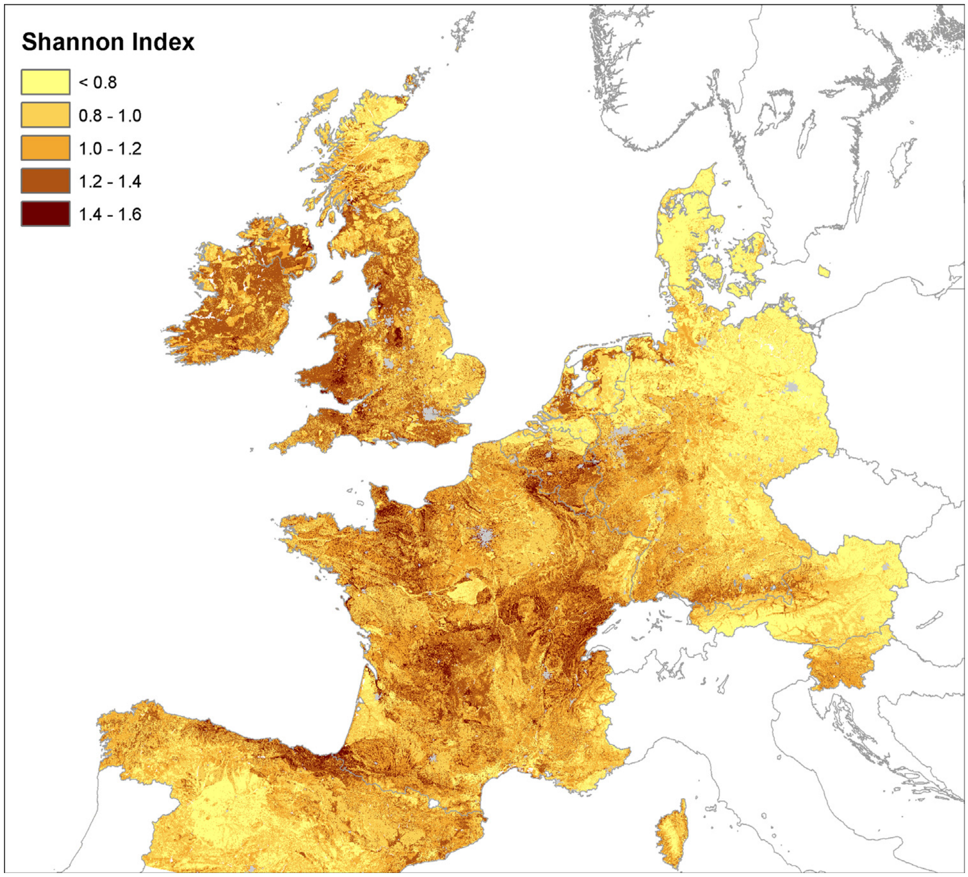

Fig. 4. Predicted diversity values (Shannon–Wiener index) of earthworm communities in Europe. See Fig. 2 for additional information.

values of the environmental predictors in comparable ranges. However, the expected earthworm distributions in these areas were indirectly derived and should hence be interpreted with great care.

3.4. Predicted patterns of earthworm distribution

The regression models (Eqs. (2)–(4) predict positive effects of all grasslands (extensively and intensively used) and negative effects of croplands, forests, heathlands and vineyards on earthworm abundance and diversity, which is in line with known habitat preferences of earthworms (Lavelle, 1983). From the land-use map of Europe, it was calculated that Ireland and Northern Ireland had about 4 times more grasslands than the combined area of croplands and forests (these three land uses account for most of the total surface in most countries) while The Netherlands had approximately equal areas of grasslands or croplands and forests combined, whereas all other contributing countries had 3 to 4 times less grasslands than croplands and forests. Therefore small-scale (local) patterns clearly emerged due to differences in habitat characteristics throughout Europe (Fig. 2). According to literature expectations (Lavelle et al., 1997), our regressions predict a slightly higher number of earthworms (28 m^{-2}), a lower number of taxa (0.6) and no effect on Shannon in agricultural grassland in comparison to semi-natural grassland. Consequently, an unexpected occurrence of earthworm hotspots due to incorrectly assigning these two grasslands types seems to be small (Table 3). In The Netherlands the differences in earthworm communities of these grasslands are larger: 55 m^{-2} for abundance and 1.9 for diversity; Rutgers et al., 2008). In summary, the level of fertilization is also a key factor in grassland management for predicted abundance of earthworms at European scale.

The large scale distribution of earthworm densities also emerge through positive correlations with latitude and longitude and climate factors (Eqs. (2)–(4); Fig. 2). Also Mediterranean conditions strongly affected the occurrence, abundance and diversity of earthworms, with local populations of 2–3 taxa far below 50 individuals m^{-2}. In the northern latitudes, the predicted abundance of earthworms was less than 5 individuals m^{-2} for some agricultural fields and most highlands in Scotland (Fig. 2, Eq. (2)). The number of different species recorded across countries was notably different (Fig. 3, Table 3), but unrelated to the abundance. This contrasts with most literature stating that positive correlations between biodiversity and abundance are expected from macroecology (Mulder et al., 2012 and references therein). France had the highest number of unique species (109 taxa) but an average density of earthworms (61 individuals m^{-2}; Table 3), whereas The Netherlands had less species but a higher abundance (Fig. 2). It should be mentioned that French data are mostly from ECORDRE database (82%) which shows a low density of earthworms all over France contrasting with data from EcoBioSoil (Cluzeau et al., 2012), and therefore strongly impacts the French earthworm density average.

Given a direct correlation as in the case of Ireland (high number of individuals and taxa; Figs. 2 and 3), one explanation came from macroecology. For instance, the Atlantic Ocean seemingly contributed to the strong correlations between diversity and abundance in Ireland and Northern Ireland, even if some of the distinctive species are known to only occur in the South (e.g. *Lumbricus friendi*, *Allolobophora cupulifera*, *Prosellodrilus amplisetosus*). On one hand, it must be mentioned that most surveys in Northern Ireland took place either in the winter (27.4%) or in the spring season (46.5%), whereas most of the surveys in the Republic of Ireland took place in the autumn (86.1%). This disparity in protocols interacts with macroecological signals and explains why the predicted earthworm community can be so diverse for the entire island of Ireland; such a North to South divergence can be namely ascribed to the occurrence of species unique to a particular data set (Appendix A: Fig. S1). On the other hand, it must be pointed out that soil quality attributes, like soil C:N ratios (known to influence both earthworms' abundance and biodiversity), are strongly correlated to latitude in Ireland (high C:N ratios at higher latitudes, and low C:N ratios at lower latitudes, exhibiting a $p < 0.0001$; Mulder et al., 2015). This study provides therefore an example of how robust predictors, as climatological and geological factors, can dilute the bias due to different sampling periods.

As a matter of fact, the mapping of adjacent regions from independent surveys using different sampling protocols, as in the case of Brittany (RMQS) versus the rest of France, or Northern Ireland versus the Republic of Ireland, did not result in artifactual outcomes when large-scale models were run, although mapping country-specific data often did (Appendix A: Figs. S1 and S2). For instance, a higher earthworm biodiversity in the alluvial plains identified from the country-specific data sets of Germany and France (Figs. S2) proved to be artifactual, due to fewer sites in each set (Figs. 1, 3 and 4). However, in smaller areas with shorter environmental gradients but a high record density like Brittany in France and The Netherlands, most differences between the regressions run at European level and their local (country-specific) models become negligible. The additional value of high record densities is recognizable also at species level, as for *Aporrectodea caliginosa* (Fig. S3) and, to a lesser extent, for *Lumbricus terrestris* (Fig. S4), which can easily coexist due to their ecological disparity (Räty, 2004).

Either effects of bedrock types or land use were recognizable for Scotland and Brittany in France (Jones et al., 2005), where middle abundance values for Brittany (Fig. 2) and lowest abundance values for Scotland pointed in both cases to relative greater species richness (Fig. 3) and higher Shannon indices (Fig. 4). Latitude is usually correlated with inverse gradients of diversity (the so-called Rapoport's rule; Brown and Gibson, 1983), a distribution that has been recognized also for earthworms (Lavelle, 1983; Mathieu and Davies, 2014), although multiple other factors can be responsible for this general pattern (Gaston et al., 1998; Willig et al., 2003). This expected latitudinal gradient is nearly visible in Fig. 3, despite lower taxa predictions in Denmark and NE Germany, but it cannot be excluded that the effect of small earthworm sample size in the surveys was hiding this latitudinal gradient, as on average abundances at low latitudes were lower than at higher latitudes (Fig. 2), aside Scotland. Furthermore, the latitudinal gradient in earthworm richness was much better detectable with a Poisson distribution than with the here used Gaussian distribution (being the coefficients of determination by a Poisson distributed GLM 27.26 for biodiversity and 40.38 for abundance).

Despite the fact that our maps were not primarily produced for any specific hypothesis testing, the different statistical and geographical distributions underpin the ongoing debate on the possible artifactual nature of the Rapoport's rule, at least for earthworms. This is consistent with geological and climatological patterns of the investigated areas, and partly consistent with the patterns observed in previous studies (Standen, 1979; Trigo et al., 1988; Monroy et al., 2003; Novo et al., 2012). Interestingly, geological history (Dercourt et al., 2000) does not seem to be as relevant for our pan-European study in comparison to that of a single country (France; Fig. 4) as reported by Mathieu and Davies (2014). One of the main differences between the data sets was the type of records used: the presence/absence (occurrence) binary data in the work by Mathieu and Davies (2014) or the demographic (density) continuous data used here.

3.5. Uncertainty

Maps remain uncertain because of the extrapolations which are needed to get a sufficient resolution for practical application and information transfer. These European maps (Figs. 2, 3 and 4) and the case studies (Appendix A: Figs. S1 and S2) are no exception to this rule, and additional sources of uncertainty originating from a lack of soil biodiversity data and differences in data quality as described above. Another not yet mentioned source of uncertainty originates from the digital maps containing the quantitative data of the predictors.

The working hypothesis is that these maps are reliable and underpin the rationale of application of the DSM approach. However, for some regions and areas this might be questionable. For instance, in the most southern region of The Netherlands (Loess area) the soil organic matter content is on average 4.6% (Rutgers et al., 2009), but in the European map this value is in the range of 1.7–2.5%, i.e. 2 to 3 times lower (Jones et al., 2005). Obviously, when predictors are not correct or properly mapped, the predictions in that specific area will be affected as well.

Despite the aggregation of many sources of uncertainty into maps (including those from miss-identifications and differences in methods), these maps should still be considered as the most reasonable outcome of a transparent process based on empirical biodiversity data, but further improvements remain possible and are desirable, if we want to further elaborate the actual earthworm demographics. As example, improvements will be done by the updating of national database, such as EcoBioSoil which will provide 1000 new data integrating earthworm data and all environmental data.

4. Conclusions

Earthworm communities in Europe were successfully mapped on the basis of harmonized data from 8 countries, and statistically significant multiple regression models. Our assembled database included more countries and covered a larger latitudinal span than previous studies on earthworms in Europe; therefore, we believe that these geographical patterns are representative for continental and possibly even for global biodiversity scales. In addition, we noted an inverse latitudinal gradient in earthworm abundance, and land use, vegetation, soil texture, organic matter and soil pH which are known to strongly affect earthworm communities (Jänsch et al., 2013; Rutgers et al., 2009) and defined their actual niche distribution on a continental scale (i.e., their habitat–response relationships) in a comparable way to other soil taxa (e.g. nematodes; Wall et al., 2002; Mulder et al., 2003, 2005).

Despite the different sampling methods and sample sizes, earthworm abundance followed the large-scale geological and climatological patterns closely, highlighting the robustness of the European models notwithstanding differing number of data sets analysed per geographical unit. Earthworm maps on a larger scale, in contrast to fine scale country maps, reflect biogeographical patterns that can be explained from earthworm distributions, their habitat requirements and climate responses. To our knowledge, these maps are the first large-scale maps that predict a soil biodiversity attribute based on multiple data sets. This demonstrates the feasibility of combining soil biodiversity data of different origin and quality for robust large-scale mapping. Such maps can fulfil different objectives, e.g. educational purposes, awareness raising, stimulation of monitoring soil biodiversity

(Global Soil Biodiversity Atlas), and the assessment of soil natural capital and ecosystem services, e.g. to contribute to National Ecosystem Assessments (Maes et al., 2013) and science-policy evaluations (Dominati et al., 2014).

We generated maps depicting the number of earthworms (adjusted to the predicted effect of habitat, position, and climate characteristics) as observed by direct (field) observation. Future studies may follow trait-based approaches facilitating a transition from taxonomic diversity to functional diversity assessment. Thus, the addition of functional or trait data, for instance those that can be derived from earthworms (e.g. life traits and functional traits such as defined through ecological groups), to future data sets and databases might reduce ongoing taxonomic controversies and will supply a comprehensive insight in ecosystem functioning and even the delivery of ecosystem services (Faber et al., 2013; Pey et al., 2014).

By merging different data sets into a single earthworm database we provided the mechanism to detect robust patterns and habitat-related distributions across Europe. We assumed that some of the larger trends are sufficiently robust at this stage, but in future, combining even more data sets with soil biodiversity attributes should lead to further improvement. For example, current methodological differences in the sampling protocol across Ireland support the need of a new, joint sampling campaign for the entire island. Moreover, we consider that this study is the first step of building a European earthworm database, which has to be reinforced but nevertheless presents the advantage to have initiated a network of earthworm data providers. The updating of the database used in this study by addition of other data from other European countries or databases (e.g. Macrofauna, Drilobase) should reinforce and consolidate this database and therefore refine the provided models. Such consolidated databases, for earthworms in particular and for invertebrates in general, will enable effective data curation, a better quality check and an improved retrieval of large data sets for better monitoring and forecasting of soil quality.

Appendix A: electronic supplementary material

The following information is supplementary to this article. The file contains national maps on the earthworm communities for The Netherlands, Germany, France and Ireland and abundances and relative abundance of two species, the endogeic *Aporrectodea caliginosa* and the anecic *Lumbricus terrestris*.

Acknowledgments

All researchers and technicians digging the insurmountable number of soil blocks, performing numerous extractions in the field, and in the lab, accomplishing harsh taxonomic identifications, provided a solid basis for the first earthworm map of Europe, and are acknowledged for their contributions. The French partners warmly thank M. Bouché for giving his huge data set and his earthworm collection to the University of Rennes. The work on data collection, harmonization, modelling and mapping was done under the umbrellas of the EU-FP7 Eco-FINDERS project (Grant number 264465) and of RIVM projects QESAP (S/607022) and BEO (M/607406), partly supported by many projects of the co authors.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2015.08.015.

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