

# Modelling of climatic tolerances of three earthworm species; *Satchellius mammalis*, *Lumbricus friendi* and *Lumbricus festivus* using Maximum Entropy Modeling

E. SHERLOCK<sup>1\*</sup>, M. COATES<sup>1</sup> & Cs. CSUZDI<sup>2</sup>

<sup>1</sup>Emma Sherlock & Matthew Coates, Department of Zoology, The Natural History Museum London.  
\*E-mail: e.sherlock@nhm.ac.uk

<sup>2</sup>Csaba Csuzdi, Department of Zoology, Eszterházy Károly Catholic University, Eger, Hungary

**Abstract.** Earthworm distributions are poorly known and individual species climatic tolerances, even less so. This paper sets out to use three species with a mainly Anglo-French distribution to test out whether using Maximum Entropy Modelling (Maxent) could be useful when studying earthworm distributions. It also gives an indication of how the likely climatic changes over a 50 year period will affect them. Overall the software seems to give useful information of where across Europe a particular species will thrive, even if not currently recorded there. It gives a real insight into how particular species might be better able to survive longer drier periods than others and which are on the edge of their climatic range already. Maxent modelling was clearly successful in demonstrating that the distributions of the ecologically different earthworm species are affected by a combination of different environmental variables. In the case of the epigeic *Satchellius mammalis* they are the annual temperature range, the precipitation of the driest month and the mean annual precipitation, for the epi-endogeic *Lumbricus festivus* they are the precipitation of the driest month, the precipitation of the wettest month and the annual temperature range. For the anecic *Lumbricus friendi* the most important environmental variables proved to be the annual temperature range, the mean diurnal temperature range and the precipitation seasonality.

**Keywords.** Annelida, Oligochaeta, distribution, climate change, range shift.

## INTRODUCTION

It is well known that different earthworm species have very different environmental tolerances (Lee 1985). For example some earthworm species have cocoons that are more frost resistant, others more drought resistant (Holmstrup 1994). To predict the possible impact of climate change software such as Maxent (Phillips *et al.* 2006) developed by the American Museum of Natural History, can be used. This software allows the input of detailed maps of environmental variables as well as the location data of specimens. Using Maxent, and suitable environmental variables, it is also possible to model the effects of future climatic conditions on the suitability of different environmental locations for the different earthworm species. Consequently, potential future predictions with regards to habitat change or climate change could be considered.

Maxent was successfully used to predict the distribution of an endogeic earthworm *Hormogaster elisae* Álvarez, 1971 in central Spain using climatic and soil variables (Machán *et al.* 2015). Latif *et al.* (2017) used Maxent to model the distribution of the epigeic sibling species pair *Eisenia fetida* (Savigny, 1826) / *Eisenia andrei* Bouché, 1972 in Iran and showed that the most important environmental variables in determining the natural distribution of *E. fetida/andrei* were annual mean temperature and precipitation in the driest months followed by the mean diurnal range of temperature and precipitation in the wettest months. Also, using Maxent modelling Geraskina & Shevchenko (2019) successfully demonstrated that the main climatic factor influencing the distribution of the two epigeic species *Dendrobaena octaedra* (Savigny, 1826) and *D. attemsi* (Michaelsen, 1902) in the northwestern Caucasus

is the precipitation in the driest month which has an effect on the desiccation of the litter layer and so on the survival of the epigeic worms in the driest summer months.

With ever increasing understanding of the importance of earthworms as ecosystem engineers (Lavelle *et al.* 2016), understanding the likely effect of climate change on distribution of individual species is crucial. However, testing of environment modelling like Maxent on continental scale data is still very rare, mainly due to the lack of continent-wide datasets.

Earthworm distribution globally is quite poorly known (Blakemore 2010). The UK, despite having a relatively small fauna with full identification keys present since the late 1940's (Sims & Gerard 1985), mirrors this poor distributional data (Carpenter *et al.* 2011). With the establishment of the earthworm society of Britain and in particular its launch of NERS (National Earthworm Recording Scheme) this situation is gradually starting to change now with over 12,000 good quality data records which together with other available datasets are analysed here.

We hope this preliminary analysis can be the beginning of future detailed continental-scale work making informed judgments on how climatic changes and habitat destruction might be affecting these important soil ecosystem engineer taxa.

## MATERIALS AND METHODS

In this study, Maximum Entropy Modelling (Maxent<sup>R</sup>) (Phillips *et al.* 2006) was used to investigate the potential distributions of different earthworm species. Using the specimen location data, as well as certain bioclimatic data that we provided, Maxent produced a map detailing the suitability of different environmental locations for each species.

*Specimens.* The data for the species used were collected in three different ways. The first was through a compilation of Museum collections data

and private research data. Specifically these were; The Natural History Museum London with collections data from the late 1800's to the present day (400 relevant records), The Hungarian Natural History Museum Budapest with collections dating from the middle 1900's to the present day (approx. 80 relevant records), The Smithsonian Institution in Washington DC with collections data from the late 1800's to the present day (approx. 25 relevant records) and 8 records of *Satchellius mammalis* from Sweden and Norway from private research data held by Christer Erseus in Sweden collected between 2008 and 2012.

For each piece of collections data which contained a vague location, an extensive search was carried out to find that location and obtain its latitude and longitude. This was not always possible. This may have been due to place name changes, or places with the same name and region such that the location given was not specific enough to differentiate, or errors in recording the location given. In such cases, that data record was disregarded.

Alongside collections data, data records from the Earthworm Society of Britain were also used to provide detailed information about earthworm populations in Great Britain. This data includes some historical records but most records were collected in the past 10 years (approx. 10,000 records). The location of sample, as well as latitude and longitude are recorded.

The third way data was collected using the book of Bouché (1972) where he recorded large amounts of location data for different earthworm species across France. Although this data is now 50 years old the climatic conditions are mapped to the time recorded at so the data is still very valid. The data for the each species used in this study were compiled and latitudes and longitudes for the locations were searched via Google Maps.

Three species of earthworms were selected for detailed mapping across Europe; *Satchellius mammalis* (Savigny, 1826), *Lumbricus friendi* (Cognetti, 1904) and *Lumbricus festivus* (Savigny,

1826). These species were selected because their restricted ranges are centering on the Anglo-French region from which the greatest proportion of our records are, and because these species had limited ranges therefore it could be deduced that they are particularly sensitive to changes in the climatic variables.

For investigating the effect of the land use on the range of widely distributed peregrine earthworms two of the UK's most common earthworm species were selected; the endogeic *Aporrectodea caliginosa* (Savigny, 1826) and the epi-endogeic *Lumbricus rubellus* Hoffmeister, 1843.

Due to the possibility of sampling bias in regards to the Earthworm Society of Britain, a map containing the location of every record of the society was also created.

*The model.* The model was created using eleven different bioclimatic variables from WorldClim 1.4, at a size of 30 arc-seconds. This was to allow high detail on smaller locations, such as the British Isles. A selection of important variables relating to both temperature and precipitation levels was chosen. The bioclimatic variables chosen were:

1. Annual Mean Temperature  
This variable shows the mean temperature of a location for a single year.
2. Mean Diurnal Range  
This variable demonstrates the mean range in temperatures on a single day.
3. Maximum Temperature of the Warmest Month  
This variable demonstrates the highest temperature that occurs in a location, in the month which is on average warmest in that location.
4. Minimum Temperature of the Coldest Month  
This variable demonstrates the lowest temperature that occurs in a location, in the month which is on average coldest in that location.
5. Temperature Range  
This variable shows the range in temperature between the average temperature of the warmest month and the average temperature of the coldest month.
6. Mean Temperature of the Wettest Quarter.

This variable demonstrates the mean temperature during the wettest three months of the year in that location.

7. Mean Temperature of the Driest Quarters  
This variable shows the mean temperature during the driest three months of the year in that location.
8. Annual Precipitation  
This variable shows the amount of precipitation a location gets over an entire year.
9. Precipitation of the Wettest Month  
This variable shows the amount of precipitation a location gets during the month with the most precipitation.
10. Precipitation of the Driest Month  
This variable shows the amount of precipitation a location gets during the month with the most precipitation.
11. Precipitation Seasonality  
Precipitation seasonality measures the variation of precipitation totals between each month over the year.

The temperature variables were chosen to reflect the effect of temperature fluctuations on the distribution of different earthworm species on different time scales. For example, Mean Diurnal Range was chosen to reflect how daily temperature fluctuations may affect earthworm distribution, whilst Temperature Range and Annual Mean Temperature were chosen to reflect how temperature fluctuations over an entire year may affect earthworm distribution. Similarly Maximum Temperature of the Warmest Month and Minimum Temperature of the Coldest Month were both chosen to investigate the possibility that some earthworms may prefer mild climates, and the effects of high and low temperatures on earthworm activity and the durability of their cocoons. For example, in the case of Minimum Temperature of the Coldest Month, this may be due to soil freezing.

The precipitation variables were chosen to reflect how the availability of moisture in the soil fluctuates through the year. Annual Precipitation was chosen to reflect how much water is available in a location during a year. The Precipitation of Wettest and Driest months was chosen to reflect how a sustained period of large amounts of water,

or lack of water, in the soil may affect earthworm populations, especially those not known to aestivate in the driest months. Precipitation Seasonality was chosen to reflect how large or small variations in precipitation over the year may affect earthworm populations.

Future projections of each of these bioclimatic variables were also used to produce the future projections of the suitability of different environmental locations for each species. Specifically we used the RCP 6.0 (Representative Concentration Pathway) pathway projected to 2050. The reason we chose RCP 6.0 is because it was the higher of the two middle RCP's, providing a possible worst case scenario, without using RCP 8.5 which may be overestimating future supply of fossil fuels (Rutledge 2011, Wang *et al.* 2017). We also did not attempt to produce maps for climate projections after 2050, due to that providing too much uncertainty.

The importance of different predictor variables for each species analyzed was determined accord

ing to Analysis of Variable Contributions (AVC). The variables that make a significant contribution to the model are those which have high values of permutation importance (PI) (Phillips *et al.* 2006).

In the case of Great Britain, land use was also investigated to ascertain whether it also has a large effect on earthworm distributions. Land use maps were taken from the Centre for Ecology and Hydrology (CEH). Land use for Ireland and Northern Ireland were not included.

## RESULTS

1. *Satchellius mammalis* shows mainly Anglo French distribution which is primarily concentrated around the Western North coast of France, the Netherlands and Belgium. According to Maxent, all regions of the UK, except exposed westerly areas of Northern Ireland, Westerly highland areas of Scotland and an area of eastern England, are favourable. Hotspots seem to be centred around South coastal regions and the Welsh English border (fig. 1).

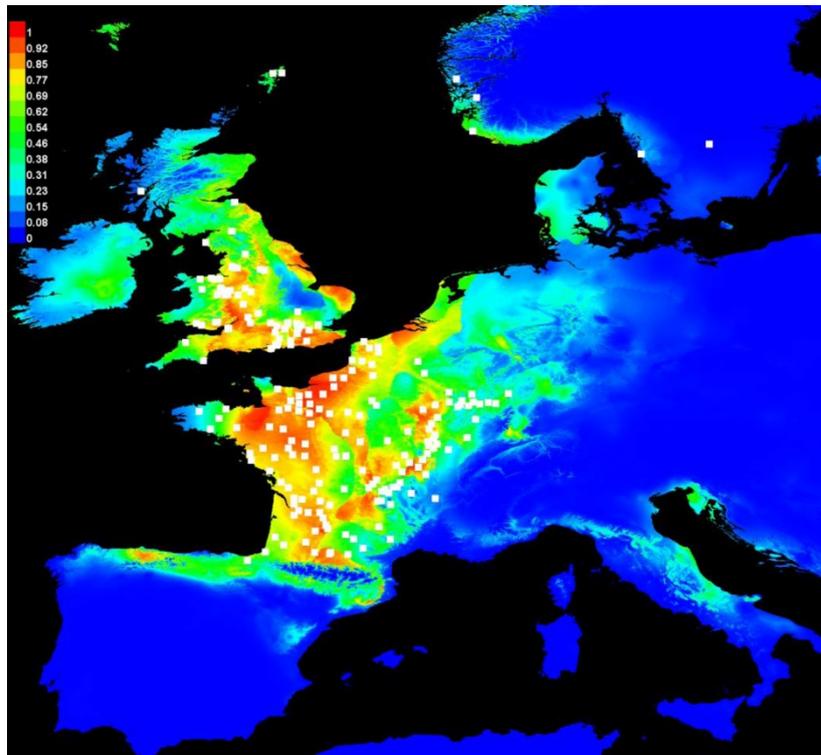


Figure 1. *Satchellius mammalis*. Present European distribution map with climatic variables.

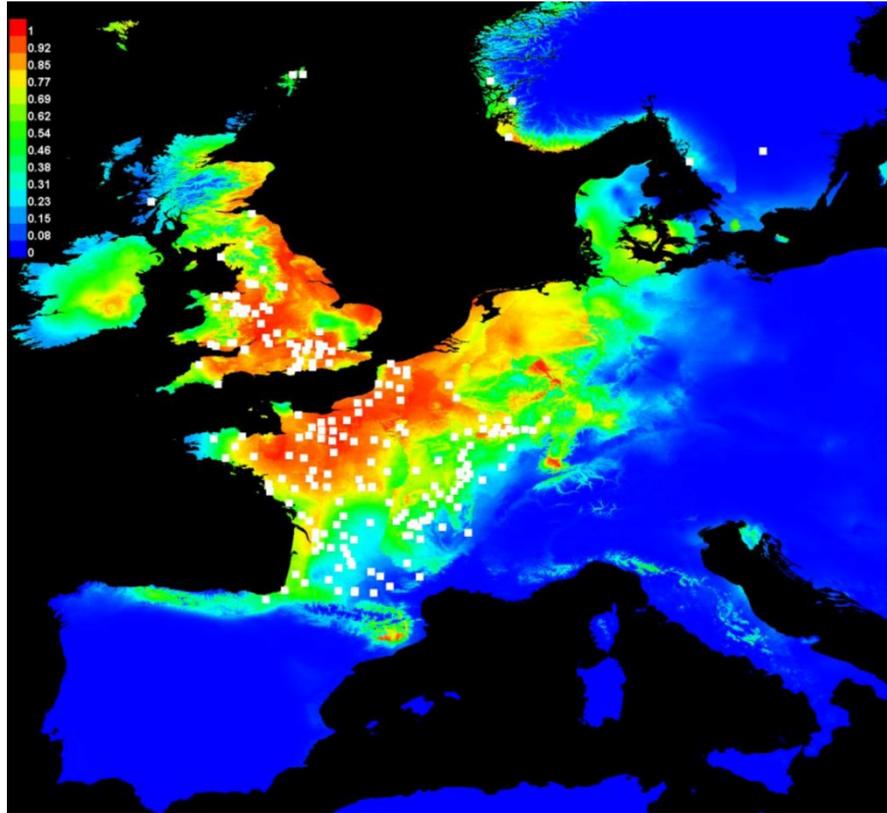


Figure 2. *Satchellius mammalis*. Predicted future European distribution map with climatic variables.

Table 1. Importance of different climatic variables in determining the distribution of *S. mammalis* according to the AVC data.

Variable	Percent contribution	Permutation importance
Temp Annual Range	39.7	43.7
Precip Driest Month	22	27.4
Mean Precipitation	1.9	9.7
Mean Temp	0.7	6.6
Mean Diurnal Range	1.5	5.1
Mean Temp Wettest Quarter	3.6	3
Precipitation Seasonality	4	2
Min Temp Coldest Month	25.2	1.3
Mean Temp Driest Quarter	0.3	1.2
Precip Wettest Month	1.1	0
Max Temp Warmest Month	0	0

The main variables determining the distributions according to AVC (Table 1) are: temperature annual range and the precipitation in the driest month. This would suggest this species is less drought resistant. It fits well to the maps produced as the area of East Anglia is one of the

driest in the country and this species seems to fare less well in those drier more easterly regions

Modelling the future distribution of *S. mammalis* shows a predicted widening of range in the more northerly regions it inhabits but the souther-

ly regions become less favourable (fig. 2). This is especially true in the UK with a predicted larger scale increase in optimal conditions like higher annual temperature in the northern regions and more precipitation in the summer.

If we incorporate in the model the UK land use map it is clear that the extent of the most favourable area for this species notably shrinks but its geographic location in the UK still remains largely the same (fig. 3).

Using the climatic predictions set in combination with the land use data a possible south western shift of the species' favourable range would appear in comparison with the modelling without land use data (fig. 4)

2. *Lumbricus friendi* distribution (fig. 5) shows that the UK is only on the very fringes of this species climatic range currently. South eastern

France, especially around the mountainous areas such as the Pyrenees and Massif Central, are favourable. A favourability towards mountainous regions is also supported by a clustering around the Alps in the East. However, they are not found in the highest altitudes of these ranges, just the surrounding areas. The most important predictors of the present distribution according AVC (Table 2) are; the temperature annual range, mean diurnal temperature range and precipitation seasonality. Future predictions with the warmer climatic conditions do not appear to be favourable for *L. friendi* (fig. 6) as the most favourable areas disappear almost entirely in the predictions, however the extent of the suboptimal areas especially in northern France and in the Ardennes, Belgium seems to be increasing. Taking into account the semi-peregrine nature of this species (Csuzdi & Szlávecz, 2004) this might indicate a possible North-Eastward shift in its distribution.

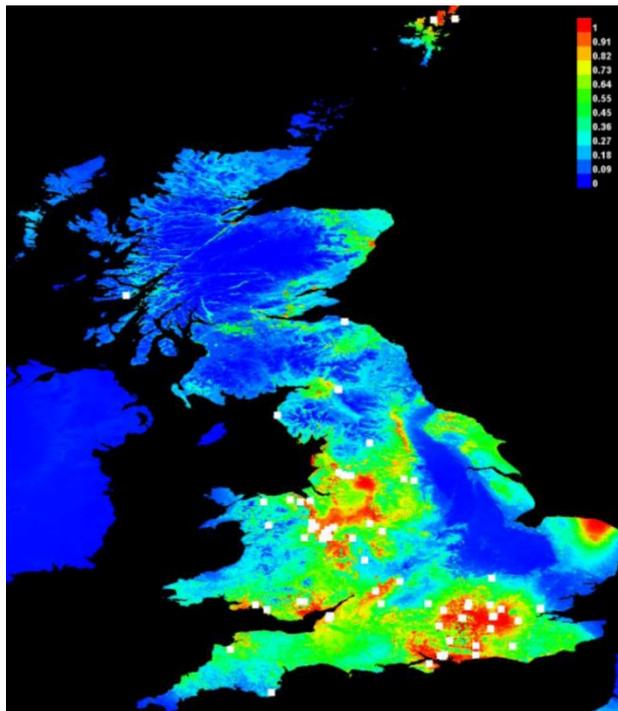


Figure 3. *Satchellius mammalis*. Present UK distribution map with the addition of land use data.

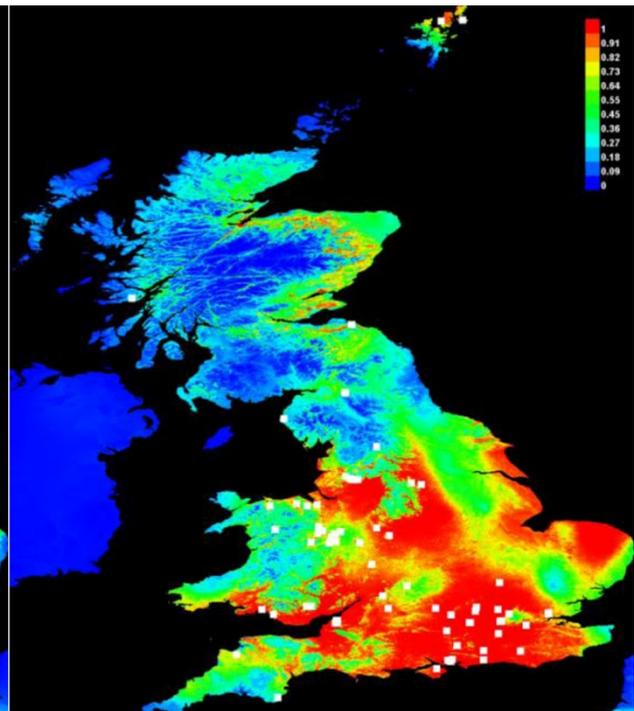


Figure 4. *Satchellius mammalis*. Predicted future UK distribution map with land use data.

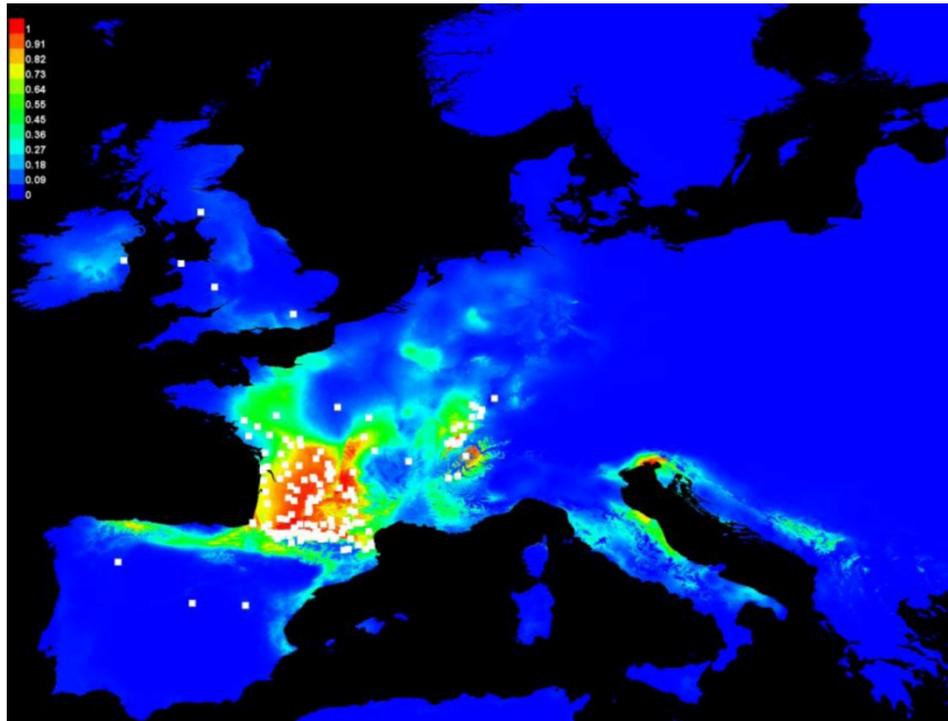


Figure 5. *Lumbricus friendi*. Present European distribution map with climatic variables.

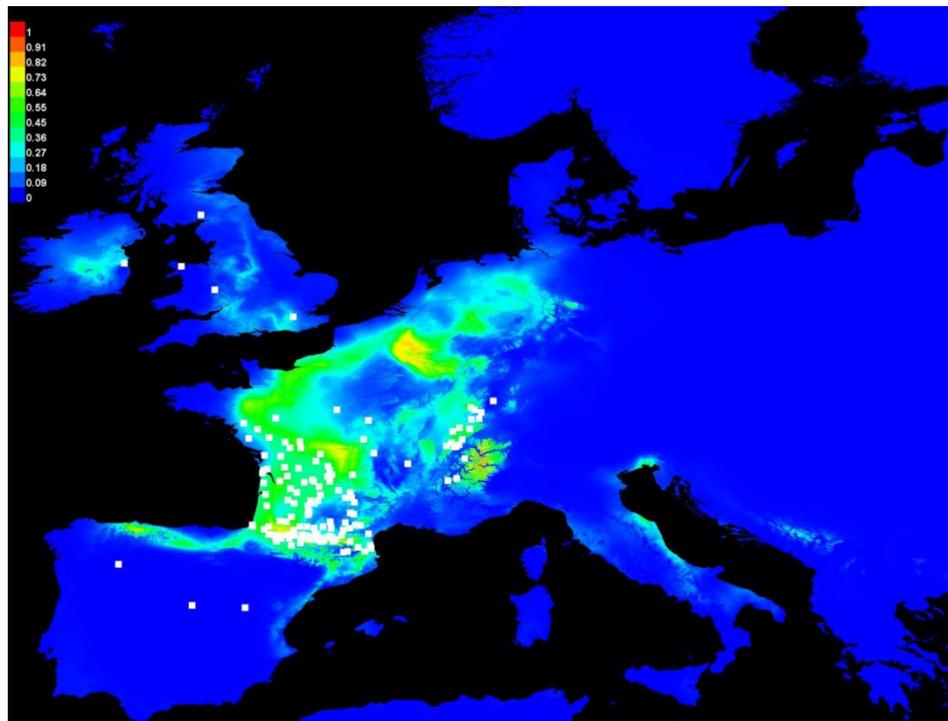


Figure 6. *Lumbricus friendi*. Predicted future European distribution map with climatic variables.

**Table 2.** Importance of different climatic variables in determining the distribution of *L. friendi* according to the AVC data.

Variable	Percent contribution	Permutation importance
Temp Annual Range	23.1	31.9
Mean Diurnal Range	22.3	24.2
Precipitation Seasonality	27.3	15.8
Mean Temp	3.9	7.7
Precip Driest Month	6.9	6.5
Precip Wettest Month	4.3	5
Mean Temp Wettest Quarter	4.8	3.6
Min Temp Coldest Month	0.4	2.3
Mean Temp Driest Quarter	5.8	1.7
Mean Precipitation	0.4	0.9
Max Temp Warmest Month	1	0.4

3. *Lumbricus festivus* shows a typical Atlantic distribution type (Csuzdi & Zicsi 2003) centring in Southern and Midland regions of the UK and the more northerly France. The major areas of unsuitability in the UK are the areas of higher altitude such as the Lake District, Pennines, Western Scotland and central Wales. A large area of eastern England is also less favourable (fig. 7).

The predicted favourable locations for this species remain mostly the same with the future predictions with indication of a slight Northern shift of its range in France and also in UK. This is especially prominent in the UK, where most of the country becomes incredibly favourable, including the previously unsuitable areas of eastern England (fig. 8). The AVC (Table 3) indicates that, like *S. mammalis*, this species is not very drought resistant. The driest areas in the UK, in the east, are areas the species is not thought to be found. The second largest factor is precipitation in the wettest month then the third is temperature annual range. So this species is very sensitive to the amount of rainfall the region has and therefore is unlikely to survive prolonged dry periods.

Incorporating the land-use data into our model shows a negative effect on the predictions, especially in a large area of Eastern England which becomes more prominently unsuitable (fig. 9). This restricted range largely overlaps with the

present distribution of the species and explains its lack from Eastern England instead of the illustrated favourable climatic conditions.

In the future prediction, as with fig. 9, larger areas of the UK become more favourable for the species (fig. 10). However, the increased favourability is more concentrated on the southern and north westerly coasts of England and the Eastern regions still remain unfavourable. This shows that land use data does have a significant negative effect on the predictions for this species, compared to fig. 8.

To demonstrate if land use has an effect on widespread species we have modelled the distribution of *Ap. caliginosa* (figs. 11–12) and *L. rubellus* (figs. 13–14) two of the most common species throughout Europe. Apart from exposed Westerly regions these species are common in most areas. According to the model predictions incorporation of land-use data makes almost no difference to the range of these species.

## DISCUSSION

The AVC tables produced by Maxent analysis proved to be very useful in determining the specific climatic conditions that each species is most susceptible to. For two of the three species analysed (*S. mammalis* and *L. festivus*) precipi

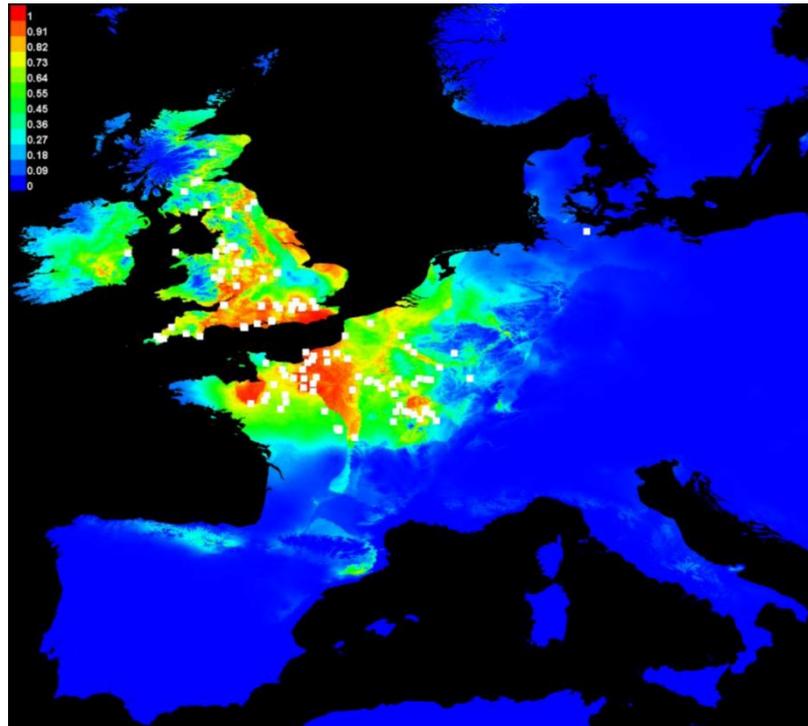


Figure 7. *Lumbricus festivus*. Present European distribution map with climatic variables.

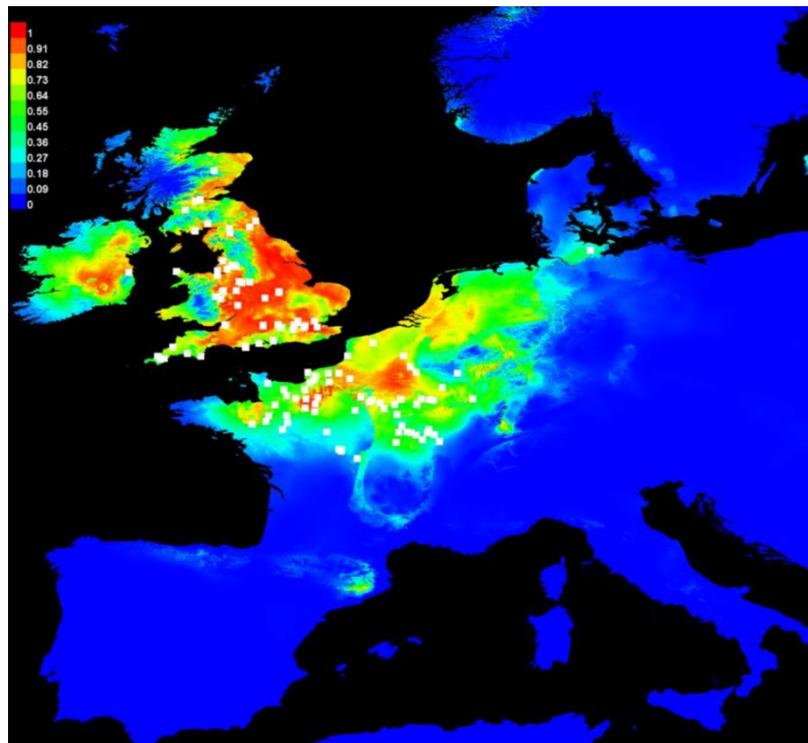
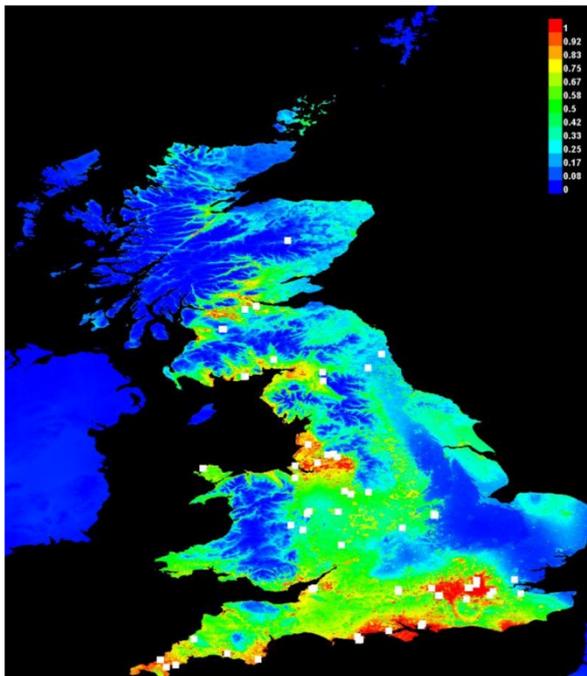


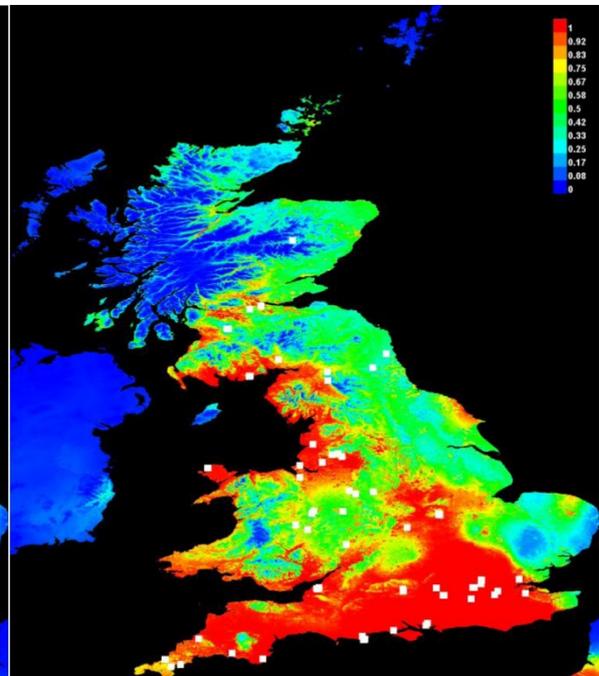
Figure 8. *Lumbricus festivus*. Predicted future European distribution map with climatic variables.

**Table 3.** Importance of different climatic variables in determining the distribution of *L. festivus* according to the AVC data.

Variable	Percent contribution	Permutation importance
Precip Driest Month	14.6	33.2
Precip Wettest Month	3.6	18.8
Temp Annual Range	41.9	17
Precipitation Seasonality	6.9	9.3
Min Temp Coldest Month	16.8	8.5
Mean Temp Driest Quarter	9.2	6.8
Mean Temp	1	2.8
Mean Temp Wettest Quarter	3.5	2
Mean Diurnal Range	0.9	1.4
Mean Precipitation	0.9	0.2
Max Temp Warmest Month	0.7	0



**Figure 9.** *Lumbricus festivus*. Present UK distribution map with land use included.



**Figure 10.** *Lumbricus festivus*. Predicted future UK distribution map with land use included.

tations in the driest months were among the most significant predicting factors, indicating that they are not drought tolerant. However, the third species (*L. friendi*) was more susceptible to temperature ranges.

Bouché (1972) in his extensive volume on the lumbricid worms of France presented an excellent

insight into the climatic tolerances of the individual species including *Satchellius mammalis*. It is a species with a healthy distribution in the UK and France, with the western and northern French coast and the southern British coast being particular hotspots. Bouché (1972) stated the species was likely to be restricted to the Northern, Western and central areas of France, not being

found below a line running from Strasbourg to Perpignan. He also stated however, that if introduced there, they would also thrive in a small area of Italy. When modelling the data available, Maxent predicted exactly that (fig. 1), so illuminating the incredible insight by Bouché but importantly also giving weight to the reliability of Maxent to correctly predict species tolerances even from a relatively small sample size.

One interesting area to explore in the UK for this species is a large area not considered habitable around Peterborough in the South, Leicester in the west, Grantham in the north and Boston in the east (fig. 3). This needs a lot more investigative work as to exactly what the factors are affecting this. We assume, especially with an epigeic species like *S. mammalis*, which is not able to aestivate in the summer, the most likely explanation would be due to this area having the driest conditions in the UK. When the potential future predictions are considered it seems that this area will become more habitable, which again could be due to a higher predicted rainfall due to climate change (fig. 4).

We considered under sampling could be skewing the presumed tolerances for this species. It is possible that the Earthworm Society of Britain does not sample as much in the east of England. To investigate this we mapped the location of every sample collected by the Earthworm Society of Britain (fig. 15). As can be seen on the map, there does appear to be a degree of under sampling in the east of England. However, we do have samples there so this alone does not explain Maxent showing a lack of suitable environmental conditions in this area. If the east of England contained suitable environmental conditions for the species, it is likely that Maxent would have predicted this based on the extensive sampling from the rest of Great Britain.

One of the rare lumbricid earthworms in Europe is *Lumbricus friendi*. There are just four records for the UK known of this species but we have numerous records from France, where the

main extent of its worldwide distribution can be found. The records however, appear only to be found in very particular habitat types, and it would seem associated with certain (not high) altitudes, and the cooler moister climates which characterise them (fig. 5). This is demonstrated by a clustering of the species around the bases of the Pyrenees, the Massif Central, and the Alps, however, not being found higher in the mountain ranges themselves. Altitude though cannot be the sole contributor to this distribution, with specimens also being found in lower lying areas further away from these mountain ranges. This species seems to be particularly sensitive to climate with a very limited range of tolerable conditions, as shown by the future predictions largely reducing its suitable habitats (fig. 6). The climatic variables which are most important to this particular species seem to be precipitation seasonality and annual temperature range. So it would appear they need a constant rainfall with limited variation between months and a low but not freezing temperature but this need a lot more investigation.

The Maxent map for *L. friendi*, a species considered recently for a red list in the UK, shows it is absolutely on the boundary of its climatic tolerances in the UK and is not a species that is suffering due to any particular habitat loss or change but a species on the absolute fringes of its ecological tolerance (and not likely to be much aided from being added to a red list) and never likely to thrive. With a species with such narrow tolerances the future could be disastrous, however the 50 years predictions again seem to be suggesting a more rosy outlook for the species in the UK albeit not anywhere else in its range (fig. 6).

It is interesting that modelling identified another highly suitable region for *L. friendi* along the Adriatic-Mediterranean region. Just recently, Stojanović *et al.* (2014) reported this species for the first time from Serbia. Although this record may be due to introduction like the North American ones (Csuzdi and Szilávecz, 2004) it also demonstrates the predicting power of Maxent analysis with its highlighting of favourable regions.

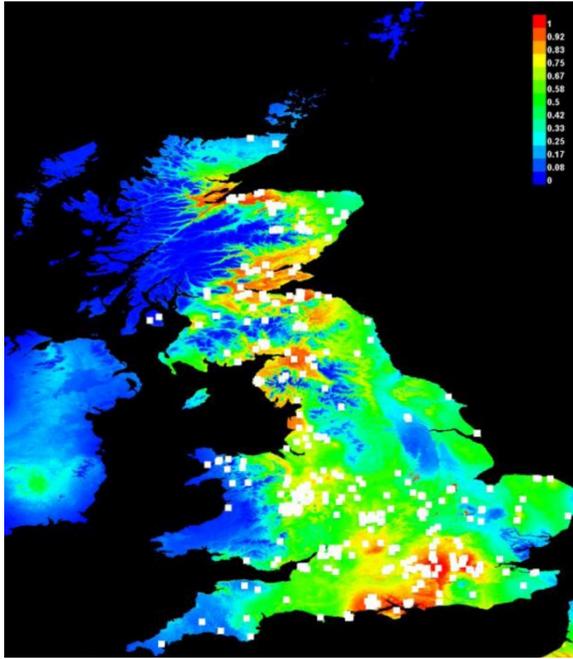


Figure 11. *Aporrectodea caliginosa*. Present UK distribution map without landuse information.

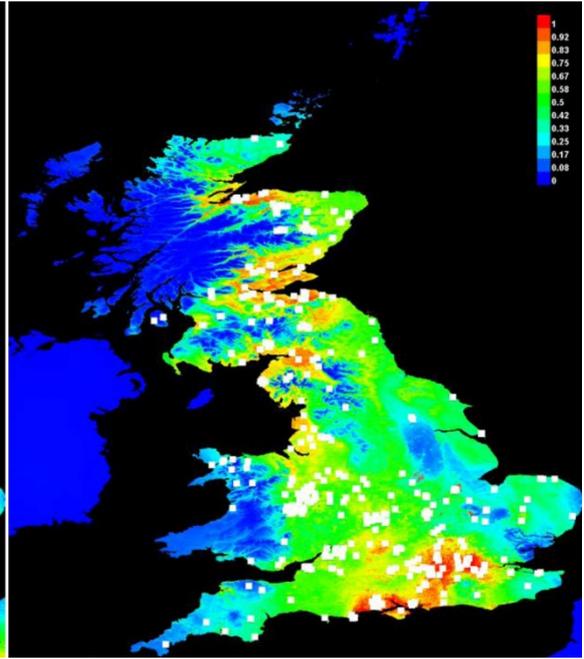


Figure 12. *Aporrectodea caliginosa*. Present UK distribution map with landuse information.

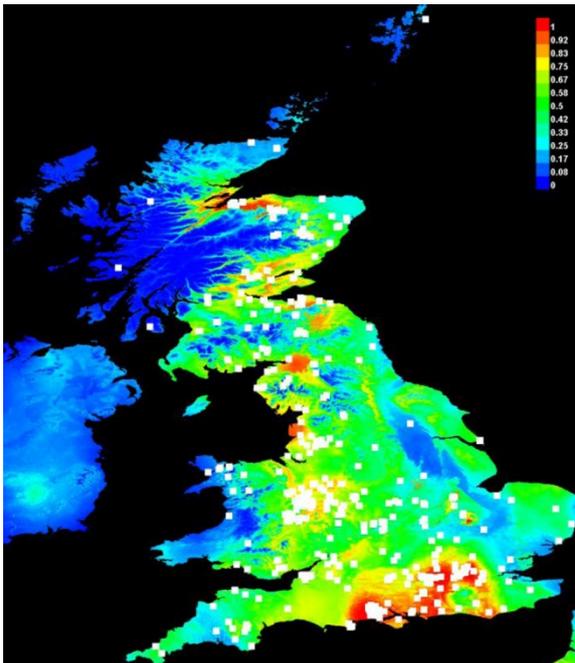


Figure 13. *Lumbricus rubellus*. Present UK distribution map without landuse information.

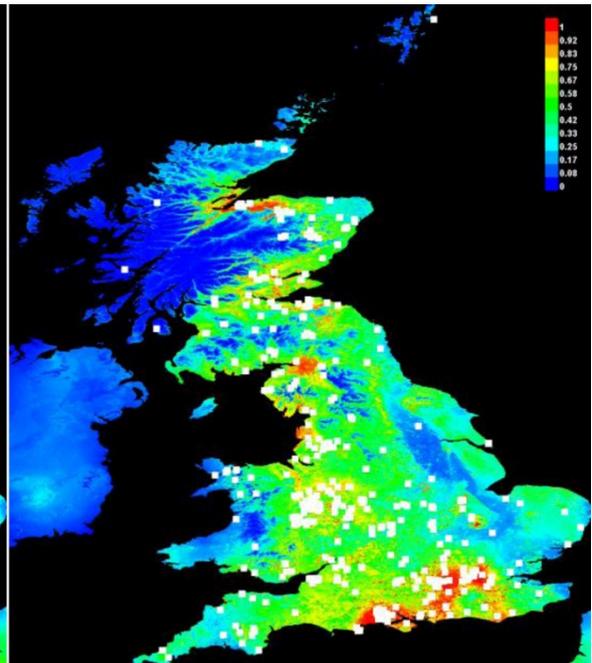
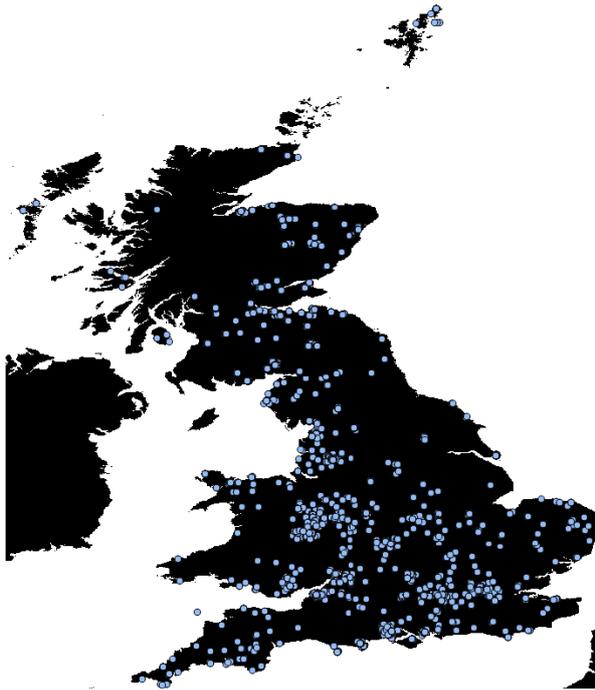


Figure 14. *Lumbricus rubellus*. Present UK distribution map with landuse information.



**Figure 15.** Map of the British Isles showing the Earthworm society of Britain's sampling localities.

Another species of interest is *Lumbricus festivus* (fig. 7). This species is not as rare as *L. friendi* however, is still considered rare in the UK. Within France it appears to have a northern distribution which is also predicted will extend out through Belgium and into the Netherlands. This would need to be tested via records from these countries. Similarly in the UK this species has a southerly distribution. It consequently appears that the areas around the English Channel and southerly North Sea seem to provide the most favourable conditions for this species. However, Maxent does also predict a very favourable channel through France running from Le Havre and the surrounding area right through to Lyon and beyond. This again would need to be explored further as this does not quite match the records produced by Bouché (1972).

But how much could land use play a role in the distribution of earthworm species? Another useful feature of Maxent is that other maps can be overlaid as well, so we used in this paper CEH land use map. Looking at very common Europe wide

species with broad climatic tolerances such as *Aporrectodea caliginosa* (figs. 11–12) and *Lumbricus rubellus* (figs. 13–14) we set to test if land-use were to affect their range. The results appeared to show there is very little difference between maps solely based on climate and when land use was added for these species. These worms can survive in most areas whether it be urban, agricultural or wild. However, when comparing this to a map of *Satchellius mammalis* (figs. 1, 3), one of the more 'sensitive' species, we can see that in this case land use has had a clear effect. Areas in the east in particular suggest a dearth of records even beyond that predicted for the dry climatic conditions alone, which our current data set supports. Looking at the land-use maps closely this seems to tie in with this species struggling in areas being converted to arable lands. However, agriculture based more on pastures for livestock do not have such a significant effect, as shown in the more westerly regions. So although this feature needs to be investigated further, in this limited study land use does seem to be a useful factor to consider for species with limited ranges. As we do not currently have detailed land use maps for Europe it might also be useful to investigate the effect of land use on the favourability of regions in France for certain species. This may be especially enlightening in the case *Lumbricus friendi*, which we know to be sensitive to climatic conditions, and may also be sensitive to different land uses.

## CONCLUSION

This is an initial study to test Maximum Entropy Modelling on a limited number of earthworm records and species. Species distribution models of course always have limitations (Jarnivich & Young 2015, Carneiro *et al.* 2016) however, the initial results do seem to indicate that Maxent is a useful tool to use in ascertaining general climatic tolerances and trends in the distribution of individual earthworm species; and that it would be worthwhile investing time and energy in a broader study with a greater number of records with a much broader geographical distribution (Rutgers *et al.* 2016)

This was especially evident with the case of *L. friendi* in the west Balkans and in France. It seems in particular to be useful with those species unable to cope with large fluctuations of temperature, or moisture. It therefore could also, when future predictions can be made of precipitation and temperature fluctuations enable us to broadly predict the likely vitality and range of these species.

Our results clearly emphasises that a lot more work needs to be carried out in collating all known verified records of European earthworm species as well as systematically collecting large quantities of species level data. From this study however, we do feel, once generated, this information alongside the use of environmental modeling like Maxent, should start to help us have a much healthier picture of how our earthworms are faring and how they are likely to fare in the future.

**Acknowledgements** – The authors would like to thank Christer Erseus for kindly sharing his research data. Bill Moser from Smithsonian Institution in Washington DC for providing collections data and Keiron Brown, the recording officer for the Earthworm society of Britain, for providing the full dataset of verified UK records.

## REFERENCES

- BLAKEMORE, R.J. (2010): *Cosmopolitan Earthworms – an Eco-Taxonomic Guide to the Peregrine Species of the World*. 4<sup>th</sup> Edition. VermEcology, Yokohama, Japan, 750 pp.
- BOUCHÉ, M.B. (1972): *Lombriciens de France: Écologie et systématique*. Annales de Zoologie-Écologie Animale, numero hors-série, INRA, Paris, pp. 671.
- CARNEIRO, L.R.A. LIMA, A., MACHADO, R.B. & MAGNUSSON, W.E. (2016): Limitations to the Use of Species-Distribution Models for Environmental-Impact Assessments in the Amazon. *PLoS ONE*, 11(1): e0146543. doi: [10.1371/journal.pone.0146543](https://doi.org/10.1371/journal.pone.0146543)
- CARPENTER, D., SHERLOCK, E., JONES, D.T., CHIMINOIDES, J., WRITER, T., NIELSON, A., BOAG, B., KEITH, A.M. & EGGLETON, P. (2011): Mapping of earthworm distribution for the British Isles and Eire highlights the underrecording of an ecologically important group. *Biodiversity and Conservation*, 21: 475–485. doi: [10.1007/s10531-011-0194-x](https://doi.org/10.1007/s10531-011-0194-x)
- C.E.H. (2018) Centre for Ecology and Hydrology, available at (<https://www.ceh.ac.uk/services/land-cover-map-2015#obtain>) [visited 14.08.2018]
- CSUZDI, Cs. & ZICSI, A. (2003): *Earthworms of Hungary*. Pedozoologica Hungarica No.1. Hungarian Natural History Museum & Systematic Research group of the Hungarian Academy of Sciences, 273 pp. doi: [10.5281/zenodo.4309820](https://doi.org/10.5281/zenodo.4309820)
- CSUZDI, Cs. & SZLÁVEZ, K. (2004): *Lumbricus friendi* a new exotic earthworm in North America. *North-eastern Naturalist*, 10(1): 77–82. doi: [10.1656/1092-6194\(2003\)010\[0077:LFCANE\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2003)010[0077:LFCANE]2.0.CO;2)
- GERASKINA, A. & SHEVCHENKO, N. (2019): Spatial distribution of the epigeic species of earthworms *Dendrobaena octaedra* and *D. attemsi* (Oligochaeta: Lumbricidae) in the forest belt of the north-western Caucasus. *Turkish Journal of Zoology*, 43(5): Article 7. doi: [10.3906/zoo-1902-31](https://doi.org/10.3906/zoo-1902-31)
- HOLMSTRUP, M (1994): Physiology of cold hardiness in cocoons of five earthworm taxa (Lumbricidae: Oligochaeta). *Journal of Comparative Physiology B*, 164: 222–228. doi: [10.1007/BF00354083](https://doi.org/10.1007/BF00354083)
- JARNEVICH, C.S. & YOUNG, N. (2015): *Using the Maxent program for species distribution modelling to assess invasion risk*. In: VENETTE, R.C. (Ed.) *Pest risk modelling and mapping for invasive alien species*. CABI, Wallingford, p. 65–81. doi: [10.1079/9781780643946.0065](https://doi.org/10.1079/9781780643946.0065)
- LATIF, R., MALEK, M. & CSUZDI, Cs. (2017): When morphology and DNA are discordant: Integrated taxonomic studies on the *Eisenia fetida/andrei* complex from different parts of Iran (Annelida, Clitellata: Megadrili). *European Journal of Soil Biology*, 81: 55–63. doi: [10.1016/j.ejsobi.2017.06.007](https://doi.org/10.1016/j.ejsobi.2017.06.007)
- LAVELLE, P., SPAIN, A., BLOUIN, M., BROWN, G., DECAËNS, T. GRIMALDI, M. JIMÉNEZ, J., MCKEY, D., MATHIEU, J., VELASQUEZ, E. & ZANGERLÉ, A. (2016): Ecosystem Engineers in a Self-organized Soil: A Review of Concepts and Future Research Questions. *Soil Science*, 181(3–4): 91–109. doi: [10.1097/SS.0000000000000155](https://doi.org/10.1097/SS.0000000000000155)
- LEE, K.E. (1985): *Earthworms: their Ecology and Relationships with Soils and Land Use*. Academic Press, Sydney, 411 pp.
- MARCHÁN, D.F., REFOYO, P., NOVO, M., FERNÁNDEZ, R., TRIGO, D. & DÍAZ COSÍN, D. (2015): Predicting soil micro-variables and the distribution of an endogeic earthworm species through a model based on large-scale variables. *Soil Biology & Biochemistry*, 81: 124–127. doi: [10.1016/j.soilbio.2014.10.023](https://doi.org/10.1016/j.soilbio.2014.10.023)

- PHILLIPS, S.J., ANDERSON, R.P. & SCHAPIRE, R.E. (2006): Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190: 231–259. doi: [10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026)
- RUTGERS, M., ORGIAZZI, A., GARDI, C., RÖMBKE, J., JÄNSCH, S., KEITH, A.M., NEILSON, R., BOAG, B., SCHMIDT, O., MURCHIE, A.K., BLACKSHAW, R.P., PÉRÈS, G., CLUZEAU, D., GUERNION, M., BRIONES, M.J.I., RODEIRO, J., PIÑEIRO, R., DÍAZ COSÍN, D.J., SOUSA, J.P., SUHADOLC, M., KOS, I., KROGH, P.-H., FABER, J.H., MULDER, C., BOGTE, J.J., VAN WIJNEN, H.J., SCHOUTEN, A.J. & ZWART, D. DE. (2016): Mapping earthworm communities in Europe. *Applied Soil Ecology*, 97: 98–111. doi: [10.1016/j.apsoil.2015.08.015](https://doi.org/10.1016/j.apsoil.2015.08.015)
- RUTLEDGE, D. (2011): Estimating long-term world coal production with logit and probit transforms. *International Journal of Coal Geology*, 85(1): 23–33. doi: [10.1016/j.coal.2010.10.012](https://doi.org/10.1016/j.coal.2010.10.012)
- SIMS, R.W. AND GERARD, B.M. (1985): *Earthworms*. Synopses of the British Fauna (New Series) 39. Linnean Society of London, 171 pp.
- STOJANOVIĆ, M, TSEKOVA, R, MILUTINOVIĆ, T. (2014): Distribution of *Lumbricus friendi* Cognetti, 1904 (Oligochaeta, Lumbricidae) at the European scale: First findings in Serbia. *Bulgarian Journal of Agricultural Science*, 20(Supplement 1):110–112.
- WANG, J., FENG, L., TANG, X., BENTLEY, Y. & HÖÖK, M. (2017): The implications of fossil fuel supply constraints on climate change predictions: A supply side analysis. *Futures*, 86: 58–72. doi: [10.1016/j.futures.2016.04.007](https://doi.org/10.1016/j.futures.2016.04.007)
- WORLDCLIM (2018): World climatic data 1.4. available at: <http://www.worldclim.org/> [visited 14.08.2018]