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Short communication

Predicting soil micro-variables and the distribution of an endogeic earthworm species through a model based on large-scale variables

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ABSTRACT

Studies on spatial patterns of distributions of soil dwelling animals have usually relied on soil micro-variables or statistical analyses based on presence/absence data. Geographic Information Systems (GIS) allow easy access to large-scale variables to build species distribution models. In this study, we used MaxEnt to model the distribution of the endogeic earthworm *Hormogaster elisae*. Significant differences were found between the predicted suitability values of localities where the species was present and those where it was absent, validating the predictive model. Most of the large-scale training variables showed significant correlation with soil micro-variables known to influence the biology of the species, proving the ability of the model to predict (to an extent) soil variables from environmental ones. The methodology could be extended to other soil fauna.

1. Introduction

Soil invertebrate fauna has traditionally been neglected by diversity and ecological research (Decaëns, 2010) due to the difficulty of sampling their populations (Smith et al. 2008). With the increasing recognition of their importance, more studies have started to explore the spatial patterns of their diversity and species distribution (Chefaoui et al., 2005; Guil et al. 2009; Crawford and Hoagland, 2010).

Concerning earthworms, both soil micro-variables and large-scale variables such as land use, lithology and climate have shown a significant effect on their distributions (Palm et al. 2013). However, most studies have relied exclusively on soil micro-variables at small scale (e.g. Joschko et al. 2006; Ouellet et al. 2008) despite requiring an intense effort to get regional coverages and being difficult to extrapolate. In contrast, large-scale variables are nowadays widely available through Geographic Information Systems (GIS), therefore facilitating the inference of species distribution models based on them (as in Shartell et al. 2013). It must be noted that the separation between both types of variables is not absolute, as some micro-variables show large-scale patterns and *vice versa*.

Other works used statistical analyses including absence data (Lindahl et al. 2009; Palm et al., 2013; Shartell et al. 2013), which are unreliable for soil fauna due to their difficult sampling. MaxEnt (Phillips et al. 2006) is an interesting statistical approach, as it is exclusively based on presence data and shows high predictive power when working with small datasets (Phillips and Dudík, 2008). It estimates the suitability of a location for the presence of a species as a function of the ecological similarity to its previously known habitat based on a set of environmental variables. MaxEnt has already been successfully implemented in soil dwelling arthropods (Crawford and Hoagland, 2010; Marek et al. 2012).

2. Model development

Hormogastrid earthworms (Oligochaeta, Hormogastridae) are especially difficult to sample due to their restricted distribution (Novo et al. 2012) and endogeic lifestyle. Obtaining distribution models that facilitate the selection of suitable sampling sites could help increasing knowledge of their currently poorly-known diversity and distribution. In this study, we chose the morphospecies *Hormogaster elisae* Álvarez, 1977 as a model system for the

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inference of suitable habitats. It inhabits relatively acidic soils (Novo et al. 2012) with extreme conditions (low organic matter, cold winters and hot and dry summers) (Novo et al. 2009, 2010) and a high percentage of coarse sand (Hernandez et al. 2003, 2007). Novo et al. (2009, 2010) established its range in Central Iberia, finding 17 populations in the provinces of Segovia, Guadalajara and Madrid. These populations were the starting point for our MaxEnt distribution model (parameters in Suppl. Material 1). The large-scale variables potentially relevant for the biology of *H. elisae* were chosen as predictor variables, reflecting the influence of extreme temperature variation and water availability across the year (isothermality, precipitation of driest month/coldest quarter and mean diurnal temperature range), lithology, land use and anthropic activities (Suppl. Material 1).

Our main objectives were i) to validate the model as a sampling site selection tool by using new presence and absence data; and ii) to find correlations between the predictor variables and soil variables (obtained from presence points). Twenty five additional presence locations plus fifty one where *H. elisae* was absent (Suppl. Material 2) were selected for the statistical validation. The mean habitat suitability values obtained for presence/absence locations were compared by ANOVA analysis to test for significant differences. Soil factors were analyzed in presence locations (Suppl. Material 1, 2) and compared with large-scale variable/suitability values obtained for each location to study their correlations; ANOVA was performed with large-scale categorical variables as grouping variables.

The geographical representation of the predicted suitability values is shown in Fig. 1.

3. Model validation and correlations

The model obtained is potentially suitable for predicting the distribution of *H. elisae*. The average test AUC (a measure of predictive performance, see Suppl. Material 1) was 0.892, showing high predictive power. In addition, the validation based on the real distribution of the species confirmed its ability to discern suitable and unsuitable sampling points, as significant differences between the predicted suitability values of absence and presence locations were found (Suppl. Material 1). The mean value for locations where *H. elisae* was found was over 0.5, the threshold established by MaxEnt for random suitability.

Both Shartell et al. (2013) and Palm et al. (2013) needed to combine locally measured variables with their GIS-generated variables to reach AUC values 0.79/0.84–0.85. This highlights the usefulness of the present model, which achieved higher predictive power while relying only on large-scale variables.

Similar success was achieved by Crawford and Hoagland (2010) when modeling the distribution of the burying beetle *Nicrophorus americanus*, obtaining higher AUC values with MaxEnt compared to other approaches. In fact, the last four years have seen a proliferation of MaxEnt-based ecological niche modeling (ENM) works in invertebrates (e.g. Muhlfeld et al. 2011; Fuller et al. 2013; Staunton et al. 2014).

False negatives (frequent in endogeic earthworms due to their deep burrowing and patched distribution) could mean some absence points were actually suitable. However, this kind of error would only affect the validation of this model, while it would hinder distribution analysis based on presence/absence data. Some

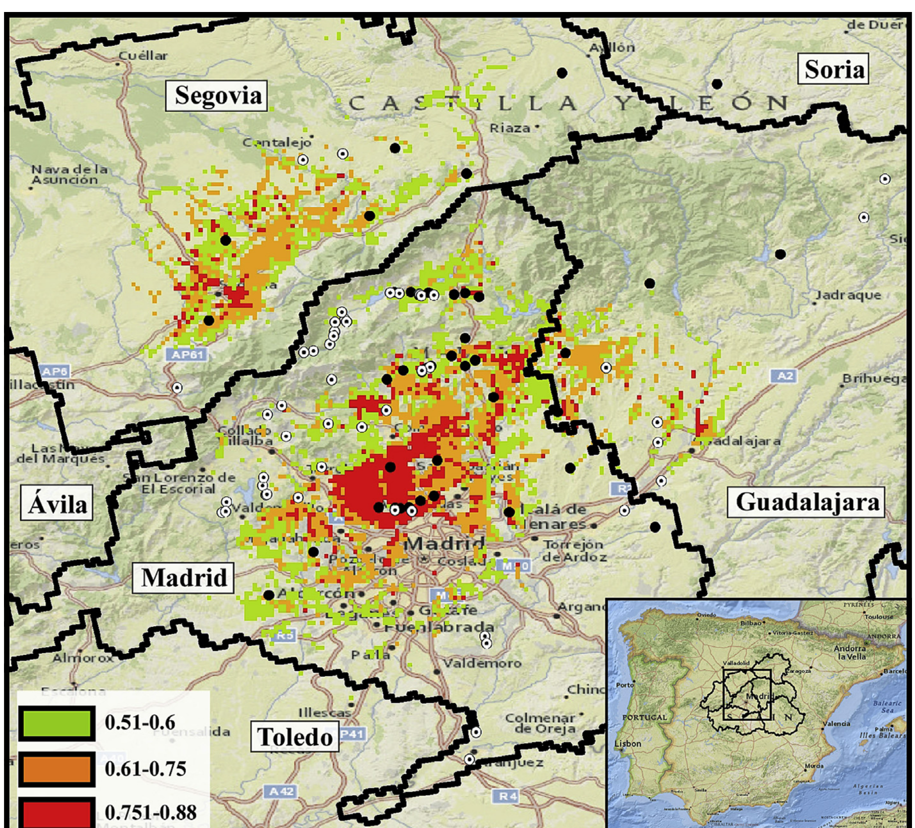

Fig. 1. Habitat suitability map including the distribution of presence (black dots) and absence (white dots) locations. Highest suitability values are shown in red, followed by orange and green. A map of the study area in the context of the Iberian Peninsula is shown for reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Correlation coefficients between soil variables, predicted suitability values and large scale variables. TRANGE: Mean diurnal temperature range, ISOTHER: Isothermality, PRDRY: Precipitation of driest month, PRCOLD: Precipitation of coldest quarter, LITHO: Lithology, VEGET: Vegetation and land use, ANTHRO: Human influence. Statistically significant values are shown in bold ($p < 0.05$). For LITHO, significant differences in an ANOVA are shown. VEGET is not shown as no significant differences were found.

		Continuous variables					Categorical variable
	Suitability	TRANGE	ISOTHER	PRDRY	PRCOLD	ANTHRO	LITHO
Coarse sand	**0.62**	**−0.67**	**−0.69**	**−0.55**	0.01	0.15	$p < 0.005$
Fine sand	0.22	**−0.39**	−0.02	−0.09	−0.15	−0.06	$p = 0.034$
Total sand	**0.66**	**−0.76**	**−0.66**	**−0.55**	−0.04	0.12	$p < 0.005$
Coarse silt	−0.29	**0.35**	**0.35**	0.17	−0.20	−0.18	$p < 0.005$
Fine silt	**−0.68**	**0.66**	**0.72**	**0.64**	0.06	−0.16	$p < 0.005$
Total silt	**−0.62**	**0.63**	**0.68**	**0.55**	−0.03	−0.19	$p < 0.005$
Clay	**−0.46**	**0.73**	**0.33**	**0.32**	0.17	0.08	$p < 0.005$
Carbon	**−0.35**	**0.55**	**0.56**	**0.64**	**0.38**	−0.15	–
Nitrogen	0.00	0.23	0.21	0.17	0.09	−0.09	–
C/N	−0.19	0.06	0.21	**0.34**	0.24	−0.08	–
pH	**−0.37**	**0.39**	0.18	0.12	−0.10	−0.17	$p = 0.028$

of the areas predicted as highly suitable could be considered potential range as opposed to the actual range of the species (false positives). Several factors such as historical limitations (failure to reach a certain area by migration, transitory flooding in the past, etc.) or anthropic modification of the habitat could explain the absence of *H. elisae*.

Overfitting issues caused by the high predictor variable/input point ratio (7/17) could be considered negligible compared to the information provided by the chosen variables. Not only were they required to cover all aspects of the earthworm's biology (the effect of large scale environmental variables being poorly known), but they also allowed to study their correlation with soil variables.

The correlation shown by high predicted suitability values and some soil parameters such as coarse soil texture, low organic matter content and low pH (Table 1) agrees with what other studies had previously proposed (Hernandez et al. 2003; Novo et al., 2009, 2010, 2012), indicating that the predictive model accurately reflects the biology of the studied species.

The correlation between the large-scale and small-scale variables studied (Table 1) can be explained from a geophysical point of view. High values of isothermality, precipitation of driest month and mean diurnal temperature range are associated with higher percentages of the thinner mineral fractions, in accordance with the promotion of mechanical and chemical weathering by increased precipitation and temperature fluctuations (Muhs et al. 2001; Schaetzl and Anderson, 2005). Significant differences between lithological categories in soil texture and pH are explained by the influence of the mineralogical composition of the parent material on soil characteristics (Whalen and Sampedro, 2010).

These correlations suggest that information provided by large-scale variables and soil micro-variables overlap, opening the possibility of predicting to an extent local variables from global, readily available ones. In our work, large-scale environmental variables are not intended to replace soil variables completely, as the model (and its predictor variables) can't explain their whole variance. Instead, the model provides a certain amount of insight into soil micro-variables while being based only on large-scale variables. After delimiting smaller sampling areas, further studies focusing on soil variables (more manageable at local scale) would help explaining the effect of spatial variability at small scale on soil fauna distribution.

4. Summary

This study highlights the potential usefulness of physical modeling to infer soil species distributions in endogeic earthworms, shown by robust statistical support and correlation with relevant soil variables. This methodology could be implemented to other soil dwelling organisms with similar limitations to the study of their distribution, facilitating their research through the systematic selection of suitable sampling sites.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2014.10.023.

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Materials and methods

Locations and sampling

Seventeen locations from Central Spain, where *H. elisae* populations were previously found by Novo *et al*. (2010), were selected as input for the MaxEnt analysis (Phillips *et al*. 2006) (Suppl. Material 2). Twenty five additional presence locations plus fifty one where *H. elisae* was absent were selected for the statistical validation (Suppl. Material 2).

Sampling was standardized to a minimum effort of 1 hour, digging in at least ten 2 m^2 spots in each 500m^2 plot.

Species distribution modeling

The following parameters of the model as implemented in MaxEnt were considered by default: a maximum number of 500 iterations, a convergence-threshold limit of 0.00001, 10,000 points as number maximum of background points and regularization multiplier equal to 1, as recommended by Phillips *et al.* (2006). Background points were randomly selected from the province of Madrid and all the surrounding provinces in central Iberian Peninsula (Segovia, Soria, Guadalajara, Cuenca, Toledo and Ávila).

Each time, a 30% of the sample records were randomly removed without replacement (through the subsample option) to be used as test points in order to measure the quality of the model, and the 70% of records were used to build the model (e.g. Tellería *et al.* 2012). The final model was constructed with the average of the replicates.

In the case of MaxEnt, the ROC-AUC technique has been used to analyze the goodness of fit of the analysis in contrast to other models of evaluation, since it avoids the problem of selecting threshold values (Lehmann *et al*., 2002) and it is capable of measuring the model ability to discriminate between the sites of species presence from the areas of absence (Fielding & Bell 1997; Engler *et al.* 2004; Elith *et al*. 2006; Phillips *et al*. 2006; Elith *et al.* 2010).

The large-scale variables potentially relevant for the biology of *H. elisae* were chosen as predictor variables to model its distribution, as described below.
Five bioclimatic variables were selected from Worldclim (http://www.worldclim.org/). Mean Diurnal Range (BIO2) – TRANGE and Isothermality (BIO 3) – ISOTHER; are suitable to represent the influence of extreme temperature variation (both daily and across the year) on earthworm biology. Precipitation of Driest Month (BIO 14) – PRDRY and Precipitation of Coldest Quarter (BIO 19) – PRCOLD; are likely to reflect the availability of water in the soil across the year, a essential requirement for earthworms. Lithology (Lithostratigraphic map of Spain, 1/200,000 scale, IGME) - LITHO was selected as topological variable, as it is likely to indirectly influence *H. elisae* ecology by determining the structure and biochemical characteristics of soils. CORINE 2006 land cover (version 12/2009: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-2009)-VEGET was chosen to incorporate information about vegetation and land use, while the 'Human footprint' data set (representing the human influence on land surface; Sanderson *et al*. 2002)-ANTHRO was selected to include the expected effect of anthropic activities on habitat suitability.
After testing for colinearity no significant correlation above 0.8 was found between the predictor variables.

Soil analysis

Soil factors regarded as most important for earthworm distribution (Edwards & Bohlen 1996; Hernández *et al*. 2003, 2007) were analyzed in 40 presence localities. When earthworms were found in different subsamples in the same locality, the soil samples were mixed. Soil texture (percentage of coarse/fine/total sand, coarse/fine/total silt, clay) and pH were measured as described by Guitián & Carballas (1976). Anne's (1945) method, adapted for a microplate reader (Microplate Bio-Rad, 590 nm) was used for organic oxidable carbon analysis using glucose as a standard, and expressed as a percentage. The Kjeldahl method was used to measure total nitrogen content as indicated in Page *et al*. (1982) and expressed as a percentage. The values are shown in Suppl. Material 2.

Statistical validation and correlation

Both ANOVA and correlation analysis were performed using STATISTICA 7 (StatSoft Inc, Tulsa, OK, USA).

Results

Species distribution modeling

Variable	Percent contribution	Permutation importance	Range

TRANGE	58,4	72,4	100-104
ISOTHER	18,7	1,9	34-35.7
LITHO	12,7	8	*
VEGET	3,3	4,3	-
ANTHRO	3,6	1,2	-
PRCOLD	2,1	3,1	-
PRDRY	1,3	9,2	-
AUC+/- SD	0.892 +/- 0.05		

Table 1. Relative contribution of each variable to the prediction model. Large variation between percent contribution and permutation importance shows the high influence of a variable on the model, as it is the case for TRANGE, ISOTHER and LITHO. The significant range for the main contributing variables is also shown. * 1-Metamorphized acid rocs, 2-Sandstones, 3-Quartzitic conglomerates, 4- Reddish arkosic lutites, 5-Arkoses, 6-Arkoses with cobble.

Statistical validation

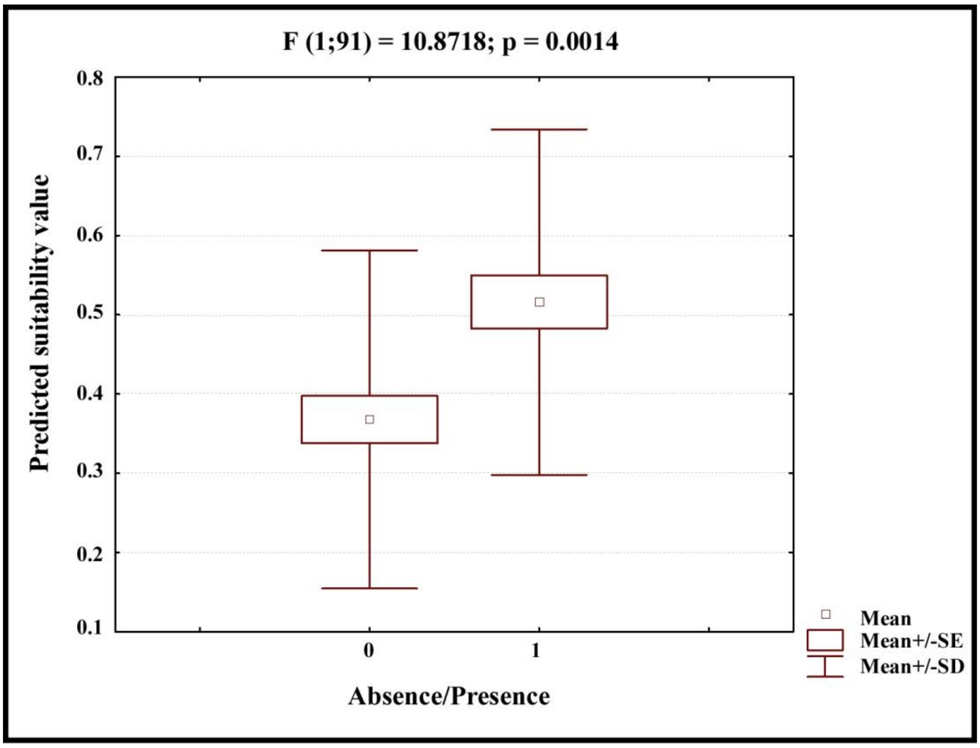

Figure 2. Box plot graphic of the predicted suitability values of absence (0) and presence (1) locations.

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Locality	Longitude	Latitude	% Coarse sand	% fine sand
Anchuelo	-3,2425	40,4806	11,69	17,48
Boadilla del Monte	-3,9250	40,4306	59,67	11,93
Cubillo de Uceda	-3,4219	40,8272	22,94	16,53
El Molar	-3,5647	40,7394	52,47	19,91
El Pardo	-3,7950	40,5197	65,51	8,65
Fresno del Torote	-3,4117	40,5975	45,34	18,24
La Cabrera	-3,6217	40,8569	65,46	9,28
Lozoyuela	-3,6211	40,9475	50,37	20,21
Navas de Buitrago	-3,5939	40,9392	51,76	18,22
Paracuellos del Jarama	-3,5331	40,5100	36,01	11,48
Redueña	-3,6017	40,8128	38,15	21,36
Saldaña de Ayllón	-3,4283	41,3864		
Sevilla la Nueva	-4,0133	40,3447	66,19	8,22
Siguero	-3,6186	41,1850	44,99	10,90
Soto del Real	-3,7783	40,7750	45,11	25,74
Tres Cantos	-3,6781	40,6128	56,29	13,16
Venturada	-3,6219	40,8019	40,69	16,85
Barcones	-2,8683	41,2983	12,34	9,21
Cabañas de Polendos	-4,1000	41,0522	48,67	17,21
Cantoblanco	-3,6844	40,5422	40,64	23,07
Congostrina	-2,9928	41,0250	20,16	16,75
El Chaparral	-3,6492	40,8222	43,72	24,10
El Cuadrón	-3,6447	40,9444	43,99	26,54
El Verdugal	-3,6947	40,9481	48,99	20,73
Guadalix	-3,7081	40,7903	56,07	15,32
Hontoria	-4,1331	40,8928	58,37	21,95
Las Colinas	-3,4367	40,7097	33,34	23,38
Lozoya	-3,7631	40,9492	50,73	24,16
Miraflores	-3,7461	40,7931	44,19	19,83
Monte Holiday	-3,7303	40,9492	50,68	18,23
Pardo 1	-3,7622	40,5189	59,07	16,02
Pardo 2	-3,7514	40,5175	63,48	14,26
Pardo 3	-3,7347	40,5194	62,10	18,22
Pardo 4	-3,7111	40,5331	59,16	14,20
Pedraza	-3,8128	41,1008	52,46	26,97
Piscis	-3,6906	40,8017	60,51	16,95
Punto 2	-3,7028	40,7953	34,16	17,87
Punto 3	-3,6997	40,7972	38,19	14,07
Tamajón	-3,2531	40,9661	13,66	14,46
Tapia El Pardo	-3,7714	40,6000		
Valderromán	-3,1192	41,3644	8,36	5,71
Valdesaz	-3,7622	41,2364	21,72	24,99
NEG1	-3,3036	40,5138		
NEG2	-3,2308	40,5726		
NEG3	-3,2369	40,6494		
NEG4	-3,2376	40,6894		
NEG5	-3,3404	40,7984		
NEG6	-2,8265	41,0986		
NEG7	-2,7843	41,1750		
NEG8	-3,7535	40,9474		
NEG9	-3,7720	40,9477		
NEG10	-3,7147	40,9450		

NEG11	-3,7135	40,9429		
NEG12	-3,7119	40,9443		
NEG13	-3,7091	40,9423		
NEG14	-3,6952	40,7976		
NEG15	-3,6923	40,8000		
NEG16	-3,7083	40,7928		
NEG17	-4,0169	40,7053		
NEG18	-3,9876	40,7235		
NEG19	-3,8882	40,7748		
NEG20	-3,7287	40,5133		
NEG21	-3,7624	40,5149		
NEG22	-4,0256	40,5633		
NEG23	-4,0978	40,5312		
NEG24	-4,0244	40,5803		
NEG25	-4,0190	40,5454		
NEG26	-4,0174	40,5460		
NEG27	-3,6843	40,9437		
NEG28	-3,8659	41,2254		
NEG29	-3,9459	41,2128		
NEG30	-4,1963	40,7584		
NEG31	-3,5822	40,2630		
NEG32	-3,5994	40,0718		
NEG33	-3,6129	40,0174		
NEG34	-3,5789	40,2484		
NEG35	-3,8281	40,6805		
NEG36	-3,8947	40,6873		
NEG37	-3,9788	40,6623		
NEG38	-3,9088	40,6012		
NEG39	-3,7794	40,7132		
NEG40	-3,9554	40,5399		
NEG41	-3,8623	40,8958		
NEG42	-4,1062	40,5095		
NEG43	-4,1002	40,5116		
NEG44	-3,8681	40,9096		
NEG45	-3,8827	40,8708		
NEG46	-3,8587	40,8910		
NEG47	-3,8922	40,8457		
NEG48	-3,8844	40,8616		
NEG49	-3,8820	40,8894		
NEG50	-3,9245	40,8328		
NEG51	-3,9443	40,8293		

% total sand	% coarse silt	% fine silt	% total silt	% clay	% C	% N
29,16	14,58	36,49	51,08	19,76	1,78	0,39
71,60	2,32	7,61	9,93	18,47	1,18	0,24
39,47	26,20	20,14	46,34	14,19	2,30	0,48
72,38	2,92	9,61	12,53	15,10	0,96	0,16
74,16	3,16	7,49	10,65	15,19	1,50	0,26
63,58	12,41	12,28	24,69	11,74	0,86	0,18
74,75	4,30	11,62	15,92	9,34	2,15	0,51
70,58	10,23	10,76	21,00	8,43	2,00	0,42
69,97	10,10	10,50	20,60	9,42	1,88	0,45
47,49	12,36	13,69	26,06	26,45	1,82	0,34
59,51	8,63	19,83	28,46	12,03	1,77	0,40
74,41	2,93	6,58	9,52	16,08	1,28	0,20
55,89	10,74	18,13	28,88	15,23	2,14	0,61
70,84	6,50	13,97	20,46	8,69	1,87	0,33
69,45	6,08	10,97	17,05	13,50	1,86	0,41
57,54	7,95	18,07	26,03	16,44	2,08	0,54
21,55	7,85	34,55	42,40	36,05	3,59	0,34
65,88	5,73	14,14	19,87	14,25	0,98	0,09
63,71	7,96	10,89	18,85	17,44	0,67	0,07
36,91	12,18	29,46	41,64	21,45	2,25	0,16
67,82	8,19	12,94	21,12	11,06	1,69	0,17
70,53	4,10	13,30	17,39	12,07	3,64	0,19
69,72	5,02	12,96	17,98	12,30	1,46	0,11
71,39	4,60	12,33	16,93	11,68	1,37	0,12
80,32	4,70	8,45	13,15	6,53	0,44	0,04
56,72	11,71	14,00	25,71	17,57	1,38	0,13
74,90	4,33	10,28	14,61	10,49	0,81	0,08
64,02	5,30	18,02	23,32	12,67	1,44	0,22
68,91	5,03	13,43	18,46	12,63	2,44	0,21
75,09	3,73	6,72	10,45	14,46	1,62	0,11
77,74	3,16	9,91	13,08	9,18	2,30	0,19
80,33	2,90	4,22	7,13	12,55	0,55	0,06
73,36	4,54	10,34	14,88	11,76	1,14	0,11
79,43	5,39	8,72	14,11	6,46	0,94	0,07
77,46	4,23	9,03	13,25	9,28	1,05	0,10
52,02	10,94	15,81	26,75	21,23	1,43	0,16
52,25	14,33	22,26	36,58	11,16	0,65	0,07
28,12	14,54	35,60	50,14	21,74	2,33	0,24
14,08	10,32	52,87	63,19	22,74	4,06	0,33
46,70	12,06	36,70	48,77	4,53	1,18	0,12

C/N	pH
4,55	7,90
4,98	6,42
4,83	5,57
5,92	6,40
5,69	6,19
4,79	7,45
4,18	5,68
4,72	5,49
4,16	5,35
5,31	7,00
4,45	7,62
6,46	5,93
3,54	5,05
5,74	5,43
4,55	6,24
3,83	7,41
10,58	7,93
11,15	7,92
9,68	5,18
14,04	8,13
9,98	6,24
19,04	5,57
13,24	7,12
11,16	5,58
10,15	6,46
10,44	6,45
10,45	5,98
6,50	5,73
11,52	5,14
14,25	6,69
12,39	7,26
10,04	7,72
9,93	8,18
12,57	5,88
10,14	6,57
8,96	7,69
8,92	6,30
9,55	8,07
12,44	7,98
10,17	7,83
