GEOGRAPHICAL PATTERNS OF THE SPECIES RICHNESS OF HELMINTH PARASITES OF MOLES (*TALPA* SPP.) IN SPAIN: SEPARATING THE EFFECT OF SAMPLING EFFORT FROM THOSE OF OTHER CONDITIONING FACTORS

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ABSTRACT. – We analysed the viscera of 534 moles (*Talpa* spp.) from 30 of the 47 provinces of peninsular Spain, including 255 individuals of T. europaea from eight provinces, 154 individuals of *T. occidentalis* from 20 provinces, and 125 unidentified *Talpa* individuals from two provinces. We identified their helminth parasites and determined parasite species richness. We related parasite species richness with sampling effort using both a linear and a logarithmic function. We then performed stepwise linear regressions to predict mole parasite species richness from a small set of selected predictor variables that included sampling effort. We applied the resulting models to forecast *T. europaea*, *T. occidentalis*, and *Talpa* spp. parasite species richness in all provinces with recorded host presence, assuming different levels of sampling effort. Finally, we used partial regression analysis to partition the variation explained by each of the selected variables in the models. We found that mole parasite species richness is strongly conditioned by sampling effort, but that other factors such as cropland area and environmental disturbance have significant independent effects.

INTRODUCTION

The European mole (*Talpa europaea* L., 1758) and the Iberian mole (*T. occidentalis* Cabrera, 1907) are two morphologically similar fossorial mammals from the order Insectivora. The former occurs throughout most of Europe, whereas the latter is endemic to the Iberian Peninsula (SW Europe). In Spain, the European mole is present in the north-central and north-eastern regions, while the Iberian mole lacks in the north-east and is especially common in the north-western quadrant (Palomo & Gisbert 2002). The two species' ranges partially overlap in northern Spain, in a sympatry area that reaches 14 administrative provinces. Soil quality and consistence and prey availability are considered the main local factors conditioning mole occurrence (MacDonald & Barrett 1993, Palomo & Gisbert 2002). The subterranean environments inhabited by moles are microclimatically stable, highly specialized and low in productivity (Elton & Miller 1954, Nevo 1979). Consequently, food availability could affect the species' spatial distribution and abundance (Nevo 1979). Moles feed essentially on earthworms, but also on larvae of beetles, flies, and other insects, and on adult beetles, myriapods, molluscs, and occasionally other small prey (Stone 1986, Castién & Gosálbez 1995, Beolchini & Loy 2004). Many of these species are intermediate hosts of heteroxenous parasites that use moles as their definitive host, so the distribution and abundance of these prey condition that of these

parasites and, consequently, total parasite species richness.

Until the present work, only faunistic and ecological data were provided about the helminths of *Talpa* species; no anterior works deal with aspects such as patterns of distribution, which have been studied in other mammal parasite species (Feliu *et al.* 1997, Goüy de Bellocq *et al.* 2002, 2003). The aims of the present work were (1) to determine the helminth parasite species richness (SR) of *Talpa europaea* and *T. occidentalis*, both separately and altogether, in a set of sampled provinces of peninsular Spain; (2) to assess the effects of sampling effort and environmental factors on the species richness observed; and (3) to predict mole parasite diversity in non-sampled provinces where the host species is present.

METHODS

The study area, peninsular Spain, covers approximately 493 000 km², which is nearly 85% of the Iberian Peninsula. It has heterogeneous climate and orography, and is relatively isolated from continental Europe by the Pyrenees, which cross the isthmus that links the Peninsula to the continent, thus restricting biotic and abiotic interchange (Bosque & Vilà 1989). Peninsular Spain is divided into 47 administrative provinces which have been used successfully as operative territorial units in a number of previous biogeographical studies (e.g. Barbosa *et al.* 2001, Márquez *et al.* 2001, Real *et al.* 2003).

Table I. – Variables used to model mole parasite species richness in the Spanish provinces. Marked with an asterisk (*) are the variables available on UTM 10x10-km squares used to model *T. europaea* and *T. occidentalis* distribution and obtain environmental favourability for the host (EFH).

Code	Variable
*Alti**	Mean altitude (m) [1]
AMax	Maximum altitude (m)
AMin	Minimum altitude (m)
*AltR**	Altitude range (m) (= A*Max*-A*Min*)
*Slop**	Slope (degrees) (calculated from *Alti*)
*HJan**	Mean relative air humidity in January at 07:00 hours (%) [2]
*HJul**	Mean relative air humidity in July at 07:00 hours (%) [2]
*HRan**	Annual relative air humidity range (%) (=|*HJan-HJul*|)
*PET**	Mean annual potential evapotranspiration (mm) [2]
*AET**	Mean annual actual evapotranspiration (mm) (=min(*PET, Prec*))
*Inso**	Mean annual insolation (hours/year) [2]
*SRad**	Mean annual solar radiation (kwh/m^2/day) [2]
*TJan**	Mean temperature in January (ºC) [2]
*TJul**	Mean temperature in July (ºC) [2]
*Temp**	Mean annual temperature (ºC) [2]
*TRan**	Annual temperature range (ºC) (=*TJul-TJan*)
*DFro**	Mean annual number of frost days (minimum temperature $\leq$ 0ºC) [2]
*DPre**	Mean annual number of days with precipitation $\geq$ 0,1 mm [2]
*Prec**	Mean annual precipitation (mm) [2]
*MP24**	Maximum precipitation in 24 hours (mm) [2]
*RMP**	Relative maximum precipitation (=*MP24/Prec*)
*PIrr**	Pluviometric irregularity [3]
*ROff**	Mean annual run-off (mm) [4]
Cont	Continentality index [5]
Humi	Humidity index [5]
*Lati**	Latitude (degrees N) [6]
*Long**	Longitude (degrees E) [6]
*Perm**	Soil permeability [4]
*DHi**	Mean distance to the nearest highway (km) [6]
*U100**	Mean distance to the nearest town with more than 100,000 inhabitants (km) [6]
*U500**	Mean distance to the nearest town with more than 500,000 inhabitants (km) [6]
DPyr	Mean distance to the Pyrenees (km)
DSym	Mean distance to a province where both moles are sympatric (km)
NFlo	Number of bioclimatic floors [7]
NReg	Number of phytogeographic regions [7]
HPD	Human population density (inhabitants/km^2) [8]
Indu	Industry density [8]
HDen	Highway density (m/km^2) [9]
RDen	Regular road density (m/km^2) [9]
HRD	Highway+road density (m/km^2) [9]
VDen	Vehicle density (vehicles/km^2) [10]
Wood	Proportion of woodland [9]
Crop	Proportion of cropland [11]
Past	Proportion of pasture land [11]
SEff	Sampling effort (different for each *Talpa* species)
EFH	Environmental favourability for the host (different for each *Talpa* species)

Sources: [1] U. S. Geological Survey (1996). [2] Font (1983). [3] Montero de Burgos and González-Rebollar (1974). [4] I.G.M.E. (1979). [5] Font (2000). [6] I.G.N. (1999); data on the number of inhabitants of urban centres taken from the Instituto Nacional de Estadística (http://www.ine.es). [7] Rivas-Martínez (1985). [8] http://www.ine.es. [9] I.N.E. (1999). [10] D.G.T. (1996). [11] I.N.E. (1996).

Between 1976 and 2002, we obtained 534 moles from 30 Spanish provinces, captured with specific traps for fossorial mammals. Of these, 255 were *T. europaea*, 154 were *T. occidentalis*, and 125 belonged to either one of these species but specific identification could not be achieved. We included them to increase the amount of data in the analysis of both *Talpa* species together. We checked the viscera of each individual for parasites, recovered and isolated all helminths found, and stored them in 70 % ethanol. For microscopical study, plathelmintes were stained in Semichon acetocarmine and mounted in Canada balsam, and nematodes were cleared in Amann lactophenol. We determined helminth parasite species richness (number of species) for *T. europaea*, *T. occidentalis*, and for *Talpa* spp. altogether, in each sampled province.

We recorded 46 variables chosen on the basis of their relation with factors potentially affecting parasite distribution and, consequently, species richness (Barbosa *et al.* 2005), namely sampling effort, topography (a surrogate for a series of environmental variables), climate, soil permeability (related with water availability), human activity, distance to the area where the two host species are sympatric, and environmental favourability for the host (Table I). Our aim was not to find the direct causes of species richness (SR) variation, but rather to make an exploratory analysis and detect relationships between SR and a series of variables that are correlated with more proximate causal factors. Statistical analyses were carried out using SPSS 11.5.

Environmental favourability for each mole species was calculated on UTM 10x10-km squares using the favourability function described by Real *et al.* (in press), the variables marked with an asterisk in Table I, and presence/absence data taken from Palomo & Gisbert (2002). We then calculated mean environmental favourability for each mole species in each province. Environmental favourability for both moles together was obtained by calculating the complementary of the simultaneous unfavourability for *T. europaea* and *T. occidentalis*, using the following formula: $F_{T.spp.} = 1 - [(1 - F_{T.eur.}) \times (1 - F_{T.occ.})]$. All other variables were obtained as explained by Barbosa *et al.* (2005). Geographical coordinates (latitude and longitude) were included to take into account spatial autocorrelation in species distributions (see Legendre 1993, Barbosa *et al.* 2003). The variables whose distributions were significantly different from normal ($p < 0.01$) according to Kolmogorov-Smirnov's test were excluded from subsequent analyses.

We assessed the relationship between parasite SR and sampling effort for each species, by regressing SR on sampling effort and on its natural logarithm (LN) separately. When the logarithmic function was more significant than the linear function, we used LN of sampling effort (instead of plain sampling effort) in subsequent analyses. We then performed stepwise linear regressions to find subsets of variables that account for the variation in the parasite SR of *T. europaea*, *T. occidentalis* and *Talpa* spp. This procedure reduces the problem of collinearity among variables, as it selects only those with the most significant contributions. We used the resulting models to predict parasite SR in all provinces with recorded presence of the host (taken from Palomo & Gisbert 2002 and from our own data), assuming constant sampling efforts of 30 and of 100 host individuals analysed per province.

Interactions between factors often result in an overlaid effect in space, so the sum of the amounts of variation explained by each variable included in a multiple regression model is usually different from the total amount explained by the whole model (Sokal & Rohlf 1981). Besides, it is interesting to discern which part of the variation in SR is explained exclusively by each of the variables included in the model, and how these variables act together affecting SR. Consequently, we performed a variation partitioning (Borcard *et al.* 1992, Legendre & Legendre 1998), a procedure useful to specify how much of the variation explained by each of the variables corresponds to its pure effect, and which proportions are attributable to the common effects of different variables.

RESULTS

Three variables (NFlo, HPD and Indu) failed the normality test and were thus excluded from subsequent analyses. The favourability (F) functions obtained for *T.*

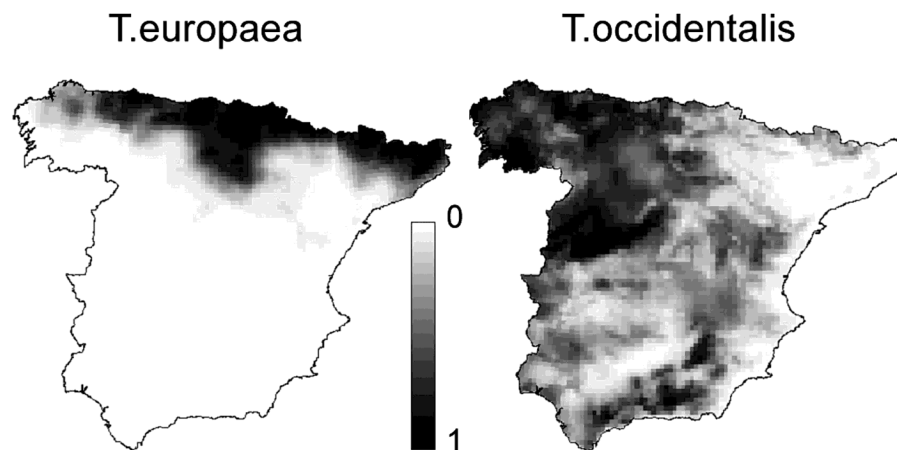## T.europaea   T.occidentalis

Fig. 1. – Environmental favourability for the European mole (*Talpa europaea*) and the Iberian mole (*T. occidentalis*) on the UTM 10x10-km squares of peninsular Spain, according to the favourability functions obtained.

Table II. – Helminth parasite species found in *Talpa europaea* (T.e.) and in *T. occidentalis* (T.o.). Presences are marked with an "x".

	T.e.	T.o.	Life cycle	Intermediate host
Trematoda				
Ityogonimus lorum (Dujardin, 1845) (Brachylaimidae)		x	Indirect	Terrestrial pulmonate gastropode_ terrestrial pulmonate gastropode
Ityogonimus ocreatus (Goeze, 1782) (Brachylaimidae)			Indirect	Aquatic snail_anelida
Nephrotrema truncatum (Leuckhart, 1842) (Troglotrematidae)			Indirect	Aquatic snail_anelida
Omphalometra flexuosa (Rudolphi, 1809) (Omphalometridae)		x	Indirect	Slugs
Cestoda				
Multitesticulata filamentosa (Goeze, 1782) (Dilepididae)	x	x	Indirect	
Nematoda				
Aonchotheca europaea Mas-Coma & Galan-Puchades, 1985 (Capillariidae)			Indirect	
Liniscus incrassatus (Diesing, 1851) (Trichuridae)	x		Indirect	
Liniscus capillaris (Linstow, 1882) (Trichuridae)		x	Direct	
Capillaria talpae (Siebold, 1850) (Trichuridae)	x		Direct	
Eucoleus oesophagicola Soltys, 1952 (Capillariidae)	x		Direct	-
Parastrongyloides winchesi Morgan, 1928 (Strongyloididae)	x	x	Direct	-
Tricholinstowia linstowi (Travassos, 1918) (Heligmonellidae) (Heligmonellidae)	x	x	Direct	-
Tricholinstowia mornanti Durette-Dessete & Vaucher, 1974 (Heligmonellidae)		x	Direct	-
Porrocaecum sp. (Ascarididae)	x		Direct	-
Spirura talpae (Gmelin, 1790) (Spiruridae)		x	Indirect	Insect
Soboliphyme occidentalis Ribas & Casanova, 2004 (Soboliphymidae)		x	Indirect	Earthworms
Trichuris feliui Ribas & Casanova, 2004 (Trichuridae)	x		Direct	-
Acanthocephala				
Moniliformis sp. (Moniliformidae)		x	Indirect	Coleoptera and Orthoptera

europaea and *T. occidentalis* were the following (variables are placed in the same order they entered the models):

$F_{T.eur.}$ = 1 - (1 / (1 + EXP(-30.029 - 0.0028 *Inso* + 0.77 *Long* - 0.35 *PIrr* + 0.024 *DFro* - 0.022 *U100* + 0.011 *U500* + 0.013 *Area* + 0.060 *HJan* + 0.017 *DPre* + 0.017 *SRad* - 0.00075 *Alti* + 0.68 *Lati* - LN(325 / 4842)))).

$F_{T.occ.}$ = 1 - (1 / (1 + EXP(13.20 + 0.020 *DPre* - 0.040 *HJul* - 0.32 *Long* + 0.59 *Perm* + 0.0013 *AltR* - 0.00085 *Prec* + 0.0099 *DHi* - 0.0063 *U100* - 0.22 *Lati* - 0.0073 *ETP* - 0.25 *TRan* + 0.0089 *Area* + 0.048 *HRan* + 0.0070 *DFro* - LN(713 / 4454)))).

The environmental favourability maps for *T. europaea* and *T. occidentalis* are shown in Fig. 1.

We found 12 helminth species parasitizing *T. europaea* and 14 species parasitizing *T. occidentalis*, in a total of 18 helminth species (Table II). By province, *T. europaea* parasite SR varied between 1 and 10, and that of *T. occidentalis* between 0 and 7. The maximum provincial sampling effort was 108 for *T. europaea*, 27 for *T. occidentalis*, and 118 for both species together (Fig. 2).

Regression analysis of SR on sampling effort revealed that their relationship was logarithmic for *T. europaea* and *Talpa* spp., but linear for *T. occidentalis* (Fig. 3). The logarithmic functions obtained suggest that, up to about 30 moles analysed per province, the relationship between sampling effort and SR is linear, as occurs with *T. occi -*

dentalis, for which the maximum effort was 27. Regression analysis using only the provinces with sampling effort lower than 35 for *T. europaea* (n = 6) and for *Talpa* spp. (n = 27) confirmed that, within this range of sampling effort, its relationship with parasite SR is linear (Fig. 3) and then it tends to asymptotize. We may reasonably expect that the relationship between parasite SR and sampling effort would also asymptotize for *T. occidental - is* with higher values of the latter. Consequently, we used a logarithmic instead of a linear function to predict the parasite SR expected for *T. occidentalis* with a sampling effort of 100 moles per province.

Stepwise linear regressions of *T. europaea*, *T. occiden - talis* and *Talpa* spp. parasite SR (TESR, TOSR and TSR, respectively) on the 43 normally distributed variables yielded the following equations:

TESR = -8.27 + 2.64 LN(*SEff*) + 0.039 *MP24*;
(R^2 = 0.97, F = 91.50, p < 0.001, N = 8) (1)

TOSR = 3.034 + 0.17 *SEff* - 5.18 *Crop*;
(R^2 = 0.70, F = 20.22, p < 0.001, N = 20) (2)

TSR = 2.094 + 1.51 LN(*SEff*) - 4.55 *Crop*;
(R^2 = 0.78, F = 47.95, p < 0.001, N = 30) (3)

The model built for *T. occidentalis* with LN(*SEff*), to extrapolate to non-sampled provinces assuming a sampling effort of 100 analysed individuals, was the following: TOSRLN = 2.99 + 1.18 LN(*SEff*) - 5.82 *Crop* (R^2 = 0.67, F = 17.079, p < 0.001).
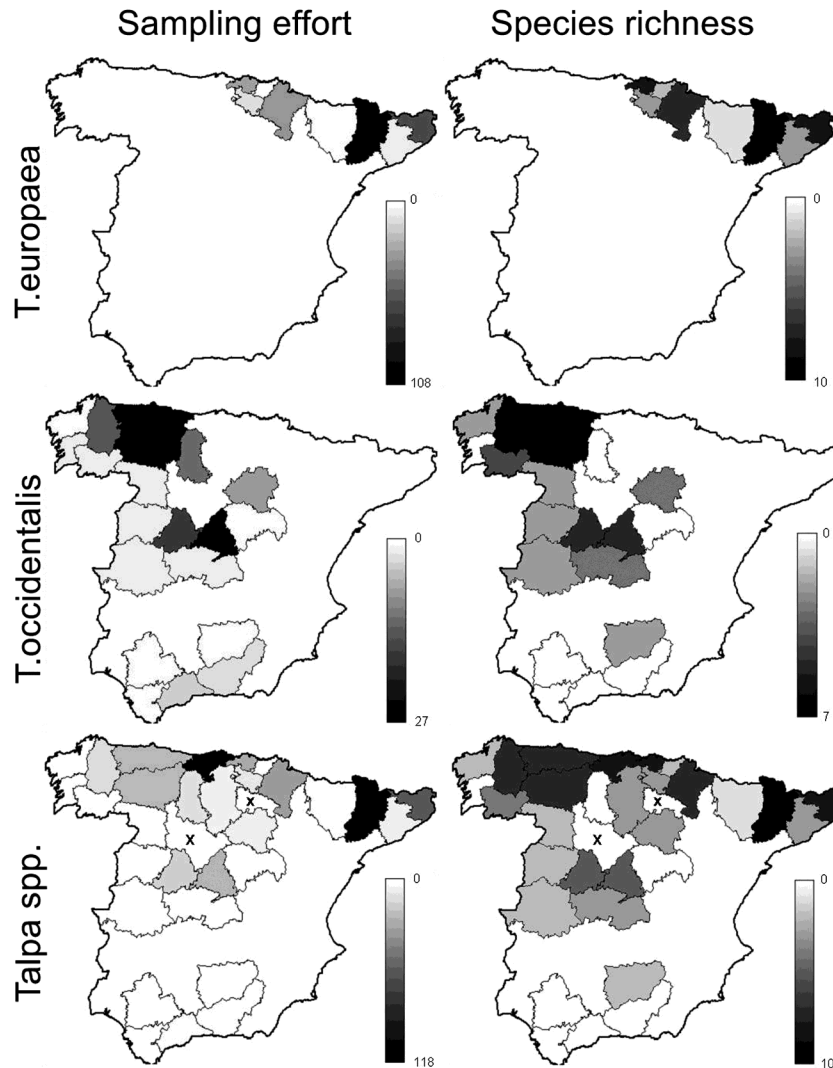
Fig. 2. – Sampling effort and the obtained helminth parasite species richness of moles, both separately and together, in the Spanish provinces sampled. Enclosed non-sampled provinces (no data) are marked with an "x". Note that the grey scale varies among provinces.

The SR values predicted by these models in the provinces sampled in each case, considering the actual sampling effort applied, and in all provinces where the host species is present assuming constant sampling efforts of 30 and of 100 analysed individuals per province, are represented in Fig. 4. The results of variation partitioning are schematized in Fig. 5.

DISCUSSION

Unlike other statistical methods such as path analysis that are based on the building of testing hypotheses, stepwise procedures are used to select subsets of relevant variables without assuming any *a priori* hypotheses. Anyway, we try to interpret *a posteriori* the variables that are included in the models.

Several authors have shown that the estimation of SR can be strongly conditioned by sampling effort (Guégan & Kennedy 1996, Feliu *et al.* 1997, Poulin 1997, 1998). Our results corroborate the importance of sampling effort for the SR encountered, but we identify other factors that have significant contributions to the models. Interestingly, the results suggest that, with more than 30 host specimens analysed, the obtained parasite SR is much less affected by effort (Fig. 3).

Stepwise regression showed that a combination of sampling effort and maximum precipitation in 24 hours accounts for 97% of the observed variation in *T. europaea* parasite SR (see R^2 of equation 1). The maximum precipitation in 24 hours is a measure of flooding intensity. Floods are a type of environmental disturbance and have been previously proposed as a controller of SR (e.g. Real *et al.* 1993). The variation partitioning for *T. europaea*

T. europaea

$y = 1.97 \, \text{Ln}(x) - 0.001$
$R^2 = 0.85$

$y = 0.19 \, x + 1.19$
$R^2 = 0.93$

T. occidentalis

$y = 1.21 \, x + 0.94$
$R^2 = 0.59$

Talpa spp.

$y = 1.71 \, \text{Ln}(x) + 0.37$
$R^2 = 0.72$

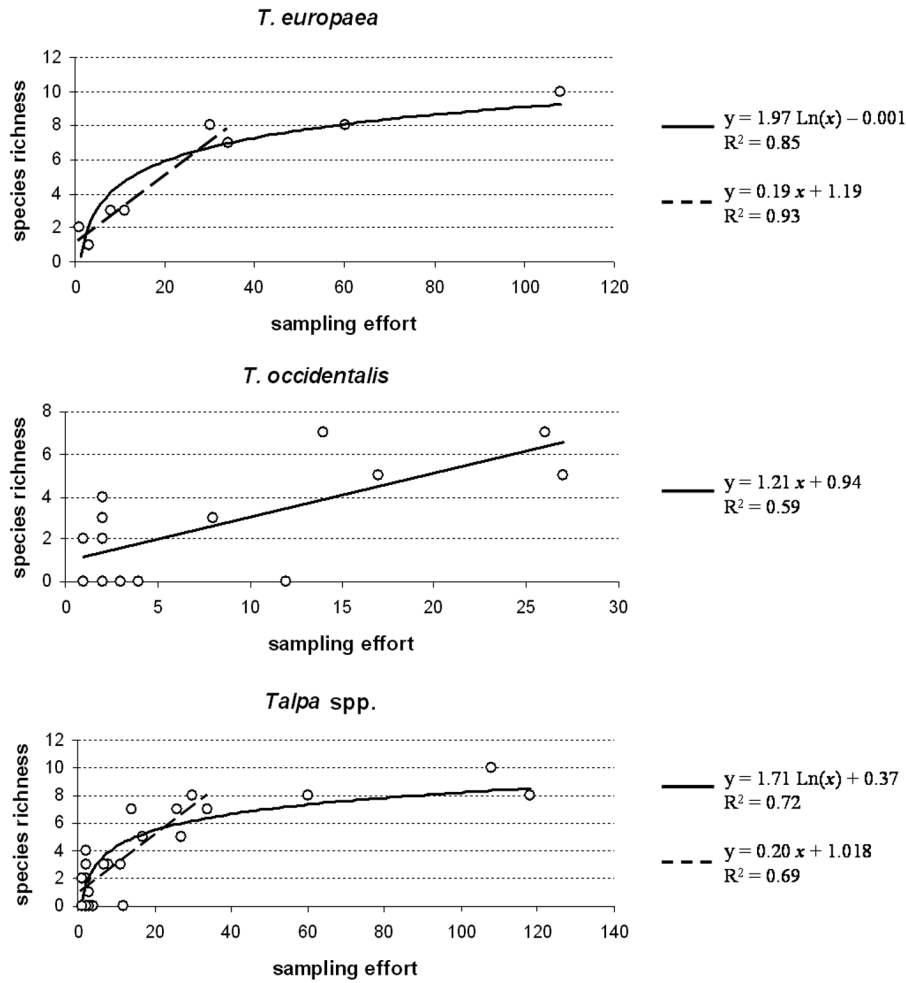$y = 0.20 \, x + 1.018$
$R^2 = 0.69$

Fig. 3. – Relationships between mole parasite species richness and sampling effort (number of moles analysed) in the provinces of peninsular Spain. Linear regressions were obtained for the provinces with less than 35 host individuals sampled (see text for details).
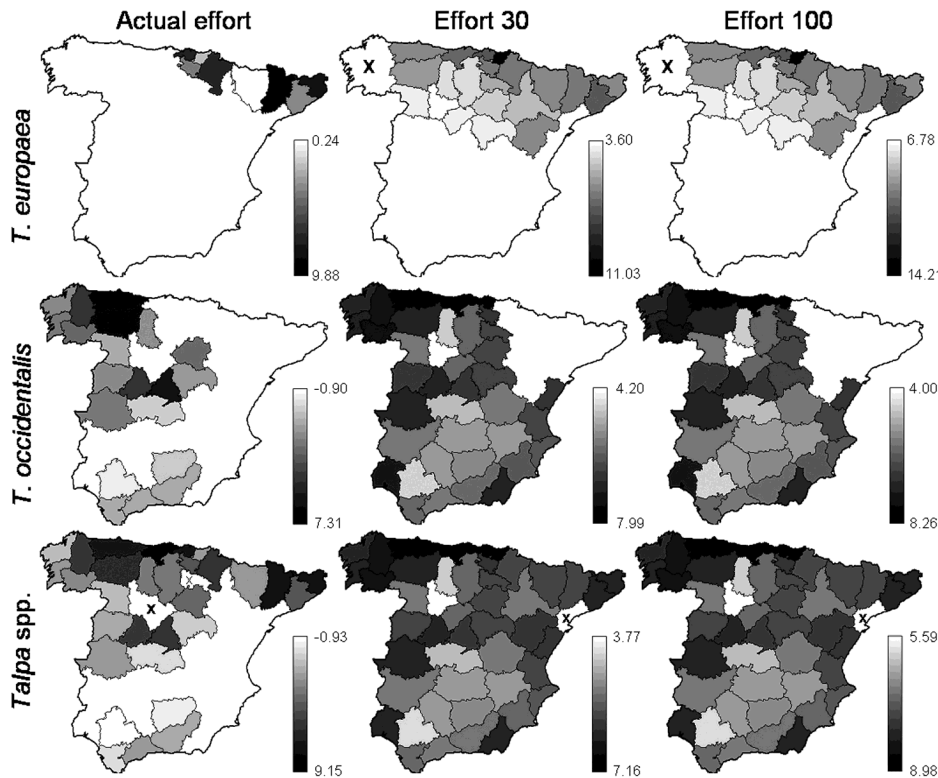

Fig. 4. – Predicted helminth parasite species richness of moles, both separately and together, considering the actual values of sampling effort employed (in the sampled provinces) and assuming a fixed effort of 30 and of 100 sampled individuals (for the provinces with recorded host presence). The "x" marks provinces with no data (host not present). Note that the greyscale varies among maps.
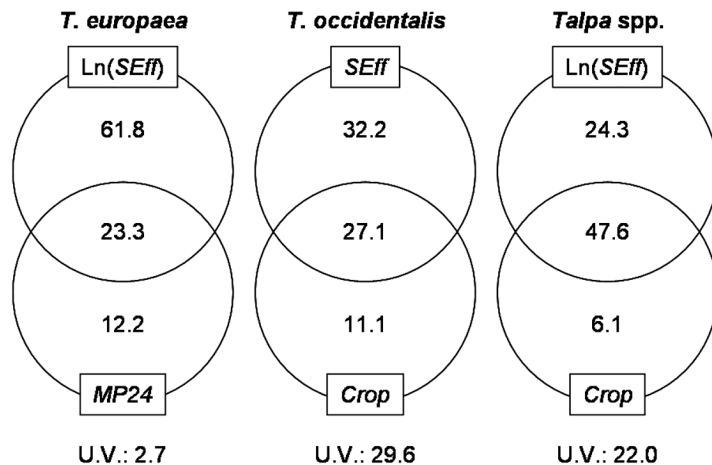
T. europaea   **T. occidentalis**   **Talpa spp.**

| Ln(*SEff*) | *SEff* | Ln(*SEff*) |

61.8   32.2   24.3

23.3   27.1   47.6

12.2   11.1   6.1

| *MP24* | *Crop* | *Crop* |

U.V.: 2.7   U.V.: 29.6   U.V.: 22.0

Fig. 5. – Results of the variance partitioning procedure for *T. europaea, T. occidentalis*, and *Talpa* spp. parasite species richness. Values in the diagrams are the percentages of the variation in species richness attributable to the pure effect of each of the variables included in the corresponding regression model, and to their common effects. U V: percentage of unexplained variation. Variable codes as in Table I.

showed that sampling effort alone accounts for most (nearly 62%) of the variation in parasite SR, but that an additional 12 % is justified exclusively by the differences in flooding intensity (Fig. 5). Besides, a supplementary 23 % of the variance is due to both factors indistinguishably, which means that the provinces where sampling effort was higher also have more intense floods (which, according to equation 1, has a positive effect on parasite species richness), thus having higher parasite SR because of these two factors acting together.

For *T. occidentalis*, sampling effort and cropland area were included in a model that explains 70 % of SR variation, with croplands having a negative effect on parasite SR (equation 2). In croplands, the abundance and diversity of arthropods and terrestrial gastropods that act as intermediate hosts for the majority of Capillarinae species, *Ityogonimus* spp., *S. talpae*, *M. filamentosa*, *Moniliformis* sp., and *S. occidentalis*, could be expectedly lower than in undisturbed, more complex habitats. The use of pesticides in agriculture could be one of the contributors to this effect. Sampling effort alone explains nearly one third of the variation, but an additional 11 % is explained independently by the differences in cropland proportion (Fig. 5). Since this variable has a negative effect on *T. occidentalis* parasite SR (equation 2) and is also negatively correlated with sampling effort ($r = -0.409$, $p = 0.07$, $n = 20$), the combined effect of cropland and sampling effort on SR is synergic and they explain part of the variation together.

For *Talpa* spp. altogether, sampling effort and cropland area account for 78 % of SR variation (equation 3). More than 24 % of this variation is accounted for by sampling effort, and cropland area accounts for another 6% independently (Fig. 5). Almost 48 % of the variation is due to these two factors indistinguishably, which means that

provinces with greater proportion of cropland (which affects SR negatively according to equation 3) have also been less sampled, so SR is affected by the simultaneous action of both factors.

Sampling effort could also be controlled using diversity indices such as Shannon's and Simpson's, which can be less affected by effort (see, for example, Barbosa *et al.* 2005). The use of estimators may avoid some spurious correlations such as the fact that it is easier to trap host individuals living in high density, and that high density also may favour the accumulation of parasite species (Guégan & Kennedy 1996). However, we have included environmental favourability for the host species as an indirect measure of abundance (Araújo & Williams 2000), and it was not selected as a significant contributor to the models.

At constant sampling effort values, the maximum number of parasite species predicted was higher for *T. europaea* (up to 11 species per province with 30 sampled individuals, and up to 14 with 100 individuals) than for *T. occidentalis* (up to 8 species in both cases) (Fig. 4). However, the high number of helminth species predicted for *T. europaea* in the province of Guipúzcoa (central north) is likely biased, since only one individual from this province was analysed and it held two different parasite species. This probably (but not necessarily) exacerbated the effect of sampling effort on the predictions for *T. europaea*.

Parasite SR of *T. europaea* and *T. occidentalis* seem to be controlled by different environmental factors and show different geographical trends. However, the joint model for the parasite SR of both species, which included 125 additional specimens from the provinces of Cantabria and Burgos (N Spain), adds predictive power to the *T. occidentalis* model (the one with the greatest number of provinces analysed) and has a considerably higher F value (see equations 2 and 3). This seems to indicate that cropland may also have an effect on the parasite SR of *T. eauropaea* that is not revealed by the few provinces analysed for this species. In addition, the mean percentage of cropland area in the provinces analyzed for *T. europaea* (21.6%) was significantly lower than in those analyzed for T. occidentalis (34.4%) ($t = -2.13$, $p < 0.05$); there might be a minimum threshold of cropland surface from which its effect on parasite SR could be noted.

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