

Deviance partitioning of host factors affecting parasitization in the European brown hare (*Lepus europaeus*)

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Abstract Deviance partitioning can provide new insights into the ecology of host-parasite interactions. We studied the host-related factors influencing parasite prevalence, abundance, and species richness in European brown hares (*Lepus europaeus*) from northern Spain. We defined three groups of explanatory variables: host environment, host population, and individual factors. We hypothesised that parasite infection rates and species richness were determined by different host-related factors depending on the nature of the parasite (endo- or ectoparasite, direct or indirect life cycle). To assess the relative importance of

these components, we used deviance partitioning, an innovative approach. The explained deviance (ED) was higher for parasite abundance models, followed by those of prevalence and then by species richness, suggesting that parasite abundance models may best describe the host factors influencing parasitization. Models for parasites with a direct life cycle yielded higher ED values than those for indirect life cycle ones. As a general trend, host individual factors explained the largest proportion of the ED, followed by host environmental factors and, finally, the interaction between host environmental and individual factors. Similar hierarchies were found for parasite prevalence, abundance, and species richness. Individual factors comprised the most relevant group of explanatory variables for both types of parasites. However, host environmental factors were also relevant in models for indirect life-cycle parasites. These findings are consistent with the idea of the host as the main habitat of the parasite; whereas, for indirect life-cycle parasites, transmission would be also modulated by environmental conditions. We suggest that parasitization can be used not only as an indicator of individual fitness but also as an indicator of environmental quality for the host. This research underlines the importance of monitoring parasite rates together with environmental, population, and host factors.

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Introduction

Parasites are defined as organisms obtaining food and shelter from another organism (host) while causing variable damage (Hudson et al. 2002). Their role in ecosystems has

been generally minimised (Tompkins et al. 2001) despite their ecological, evolutionary, and conservation relevance (Hudson et al. 2002; Thomas et al. 2004; Pérez et al. 2006).

The distribution of a parasite within a host species is not solely the result of random processes (Bordes et al. 2009). Instead, it has been associated to different exposure rates to the parasite and to variable host susceptibility to infection (Thomas et al. 2000). Gaston and Lawton (1988) and Gregory (1997) grouped the main potential determinants of parasite distribution in a specific host population into three groups of factors: host individual factors (such as age, sex, body size, diet, and immune strength), host population factors (abundance, range, and migration), and environmental factors (habitat). The interactions between different types of factors modulate parasite abundance in a given host population. In the case of parasite diversity patterns through a host species, interactions between concomitant parasites are also relevant (Telfer et al. 2008).

Though knowledge of host-parasite systems is increasing, how host-parasite interactions scale up to the host community level is still poorly understood (Hatcher et al. 2006). One level of determining factors is the host, which represents the ultimate habitat for the majority of its parasites. Hence, host individual characteristics can affect parasite occurrence (reviewed by Wilson et al. 2002; parasite species richness, Morand and Poulin 1998; parasite abundance, Patterson et al. 2008). For example, an important individual factor which has been found affecting susceptibility to parasite infection is host age (Hudson and Dobson 1995), whose influence can be related not only with immunity but also with age-dependent exposure (Cattadori et al. 2005a, b). Sex, reproductive status (Molina et al. 1999), body condition (Murray et al. 1998), or genetic variability (Cote et al. 2005) are other host factors commonly explaining parasite abundance and are frequently mediated by the host immune capacity or behaviour (Poiani 1992).

Another scale at which parasite distribution across hosts is mediated refers to host population parameters (Gregory 1997). Host population size, density, and aggregation are positively related with parasite abundance (Grenfell and Dobson 1995; Rohani et al. 1999; Acevedo et al. 2005, 2007a; Vicente et al. 2007a) as well as with parasite species richness (Nunn et al. 2003). Host social organisation (Bordes et al. 2007), including group size and gregariousness, group stability, territoriality, and social behaviour, may also modulate parasite transmission between individuals and between groups (Brown and Brown 2004). Population parameters determine the level of direct or indirect contact rates between hosts, so as the exposure to infective stages and the density-dependent individual susceptibility to parasites (Poiani 1992).

Since a large proportion of macroparasites exhibit life cycles that include infective stages off of the definitive host,

environmental factors are crucial to determine the viability and the spatial heterogeneity in the distribution of parasitic infective stages (Thieltges and Reise 2007). For example, several studies have shown that variations in the meteorological conditions have a marked influence on host exposure to parasites (O'Connor et al. 2006) by affecting free-living parasite stages (Vicente et al. 2004), parasite vectors (Sacks et al. 2003), or intermediate hosts. Habitat-related factors, such as those related to food availability, influence host susceptibility to infection, often in close relationship with population factors (Matson 2006). Therefore, fitness costs are often more evident in low host quality habitat and harsh conditions (Caron et al. 2003). According to this idea, parasites could not only reflect host individual quality (Alzaga et al. 2008) but also host population and environmental quality (Vicente et al. 2007a).

Parasite community studies have described some macroecological and spatial patterns (Poulin 2004; Guègan et al. 2005). Furthermore, parasite distribution modelling has been frequently carried out using environmental factors (Gillespie and Chapman 2006) or host individual factors (Clemons et al. 2000), but few times, a global view of this complex system has been taken into account (Nunn et al. 2003; Poulin 2007). Here, we provide an innovative approach on the host-related factors influencing parasite prevalence, abundance, and species richness in European brown hares (*Lepus europaeus*) from northern Spain. We considered three groups of explanatory variables: individual, host population, and host environmental factors. We hypothesised that parasite infection rates in European brown hares were mainly determined by host-related factors depending on the nature of the parasite (endo- or ectoparasite, direct or indirect life cycle).

Materials and methods

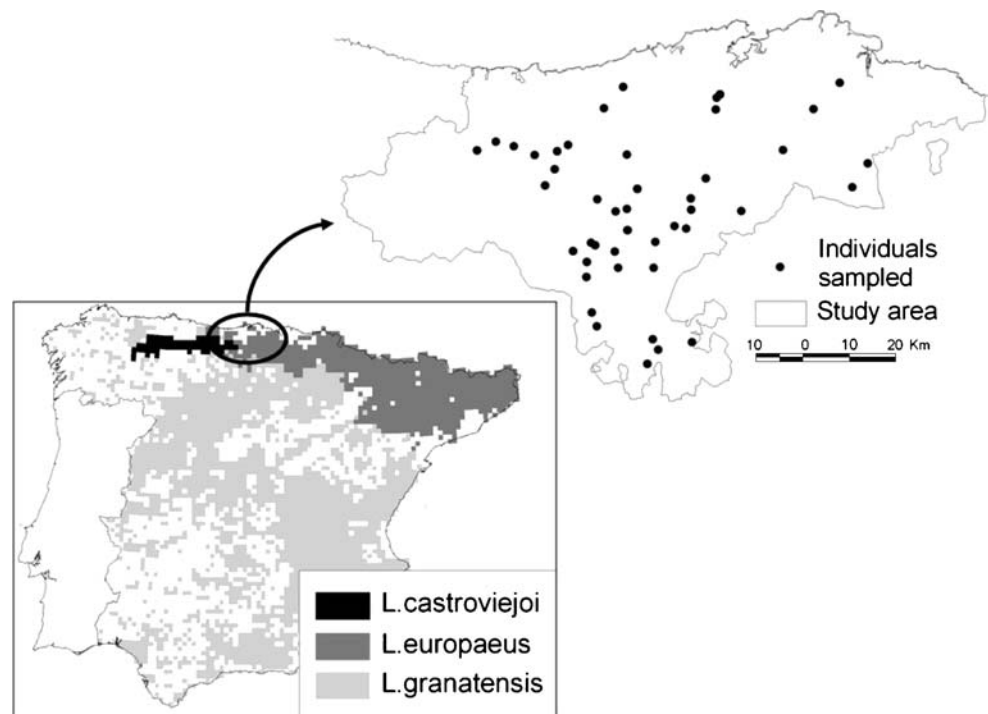
Study area

The study area, Cantabria, 532,417 km², is located in the north of Spain and represents the south-western limit of the natural distribution of the European brown hare. In this area, the European brown hare distribution is in contact with the distributions of the two other *Lepus* species endemic of the Iberian Peninsula: *Lepus granatensis* and *Lepus castroviejoi* (see Fig. 1). Cantabria is located in the Eurosiberian region and has an Atlantic climate. The predominant vegetation consists on deciduous and mixed forests with pastures and grasslands managed for cattle grazing (Moreno et al. 1990).

Sampling, individual factors, and laboratory analyses

Sixty-four European brown hares were collected from sport-hunters between October and December 2006. Samples were

Fig. 1 Location of the study area and of the sampled European brown hares. Distribution areas of the *Lepus* species were taken from Palomo and Gisbert (2002)



homogeneously distributed across the study area (see Fig. 1). The study animals consisted of 21 young hares (ten males, ten females, and one unknown) and 43 adult hares (19 males and 24 females). During post-mortem analysis, sex and age class (young, less than 7 months; adult, over 7 months) were recorded following Stroh (1931). Individual biometrics was also registered to assess a body condition index (based on body mass divided by hind-foot length, see Krebs and Singleton 1993), and spleen mass was used as immune investment-body condition indicator (Morand and Poulin 2000; Corbin et al. 2008).

We immediately inspected the head, neck, ears, and ventral surface of hare carcasses for any tick stage. These were subsequently identified as previously described by Gil Collado et al. (1979). The liver was sliced, washed, and inspected for hepatic parasites. The gastrointestinal tract was removed for parasite examination, and nematode and cestode loads were assessed by common parasitological techniques (Georgi and Georgi 1990). We divided the gastrointestinal tract into stomach and small and large intestine. The content of each part was removed into conical receptacles and allowed to sediment. Later, the supernatant was discarded, the content washed several times and, afterwards, when most of the dirt had been removed, it was meticulously inspected for nematodes and cestodes. This first inspection was carried out under a magnifying glass only to distinguish worms. Nematodes found were stored in 70% ethanol and later identified to species level by means of Anderson and Skryabin keys (Skryabin 1991; Anderson 2000). Cestodes were stored in

acetic acid-alcohol-formalin solution (Ash and Orihel 1991) and identified to family level by means of Khalil keys (Khalil et al. 1994). Coccidian oocysts of the genus *Eimeria* (Pellerdy 1974) were revealed by faecal flotation (zinc sulphate solution), counted with a McMaster camera, and expressed as oocysts per gramme of faeces.

For statistical analysis, prevalence (presence) and abundance (number of adults found in each individual or oocysts per gramme of faeces in the case of coccidia) were calculated for each taxon (Bush et al. 1997). Due to the low number of parasite taxa, we calculated simple richness indices: helminth richness, the number of helminth species present in an individual; and species richness, the number of total parasite species present in an individual host.

Host population characteristics

Cantabria is divided into 14 areas according to local habitat structure and topography (<http://www.derecho.com/l/boe/ley-12-2006-caza-cantabria>). The European brown hare is distributed in 12 of these areas, which were included in the present study. Thus, hare populations were defined on a biogeographical basis. One spotlight transect per sampling area (or hare population) was designed according to a habitat-stratified criterion. From September to November 2006, two repeats per transect were carried out to estimate hare population size in each sampling area using a handheld 100-watt spotlight and sweeping the light in a semi-circle (Barnes and Tapper 1985; Gortázar et al. 2007). A total of 817.76 km were surveyed, with an average length of

29.21 km per transect (range from 23.14 to 36.81 km). A hare abundance index was calculated as the average number of animals seen per kilometre surveyed (KAI) for each area (see details in Gortázar et al. 2007), quantified as the highest KAI obtained in the two repetitions. Mean hare abundance index obtained was 0.435 hares per kilometre surveyed (SD=0.172, minimum=0.037, and maximum=0.698). The extracted abundance indexes were reclassified into four classes based on statistic quartiles, being 1 the lowest abundance and 4 the highest.

Spotlight transects, as well as other additional surveys of pellet groups, were used to obtain hare presence data to perform the habitat suitability model (see below). Transects of pellet counts were 1 m wide and homogeneously distributed in the study area. Each transect was divided into 10-m length sectors (Vicente et al. 2004; Acevedo et al. 2007a, b). All presence data obtained were geo-referenced with global positioning system and subsequently transferred to the 500×500 m sampling grid (finally, 368 squares grid units with hare presence).

Environmental data: habitat suitability model

As the host-environment relationship was not known a priori, we used predictive habitat models to derive the macro-ecological requirements of the species from the locations in which the species occurs (Austin et al. 1990). We used the output of this kind of model, i.e., the habitat suitability index, as an index of habitat quality for the hare.

Suitability was related to meteorological, geomorphologic, and vegetation-related factors. We used ecological niche factor analyses (ENFA), a profile technique implemented in BioMapper (Hirzel et al. 2002a), for this purpose. ENFA is a method based on a comparison between the environmental peculiarities of the localities occupied by a given species and the environmental characteristics of the entire study area (Hirzel et al. 2002b). ENFA uses presence-only, presence/absence, or abundance data to compute a number of orthogonal factors from several environmental predictors similarly to the principal component analysis but looks for factors of biological significance (Hirzel et al. 2002b). Because most of the information is usually contained in a few first factors, only these are kept to compute the final habitat suitability map. The habitat suitability map is obtained as a weighted average of the partial suitabilities of each computed factor, ranging from 0 (minimum habitat suitability) to 100 (maximum suitability; see Hirzel et al. 2002b for a complete description of the process). Explained information and explained specialisation were used to measure how the resulting suitability model explained the observed data. The predictive power of the habitat suitability model was assessed by means of the spatially explicit Jackknife

cross-validation procedure also implemented in BioMapper (Hirzel et al. 2002a).

To build the habitat suitability map, the study area was divided into 500×500 m universal transverse mercator grid squares ($n=22,554$ sampling units). This was an adequate size according to the biology and ecology of the studied species (Peroux 1995). Geomorphologic and habitat-related variables were obtained from the environmental thematic cartography provided by the government of Cantabria. Geomorphology variables were calculated from a digital elevation model of 100 m pixel width. Habitat structure and composition variables were obtained from the regional geographic information systems (GIS) databases provided in vectorial format. Meteorological factors were extracted from the “Atlas Climático Digital de la Península Ibérica” (200 m pixel width; Ninyerola et al. 2005). All variables were handled and processed in a GIS environment using Idrisi Kilimanjaro v. 14.02 (Clark Laboratories 2004). Eighteen continuous environmental variables were defined for each sampling unit (see Table 1). For a similar methodological approach, see Acevedo et al. (2007b).

Deviance partitioning analysis

Imitating the scaling up of host-parasite interactions along host factor levels, we used three groups of explanatory variables (factors) to explain parasite prevalence, abundance, and species richness: individual host, host population, and host environmental factors. Individual host factors included age and sex classes, a body condition index (Krebs and Singleton 1993), and spleen mass (gramme); host population factors included hare KAI; and host environmental factors included the habitat suitability index and vegetation diversity (number of different vegetation patches in each sampling unit, grid squares of 500×500 m).

Variation partitioning is a quantitative method in which the variation of a dependent variable can be separated into independent components reflecting their relative importance. This procedure allows specifying how much of the variation of the response variable is explained by each factor group (in percent), not affected by the collinearity with other factor groups in the model, and which proportion is attributable to their shared effect, i.e., their combined effects (Legendre 1993; Legendre and Legendre 1998). The sum of the amounts of variation explained by each factor group and by the combined effects usually differs from the total amount explained by the whole maximal model, mainly due to the interactions between factors and the subsequently overlaid effects (Barbosa et al. 2005).

We partitioned the explained deviance (ED) on parasite prevalence using generalised linear models (GLM, Statistica 6.0), modelling with a binomial error and a logit link function. Similarly, we analysed the effects of the explan-

Table 1 List of variables included in ecological niche factor analyses to estimate habitat suitability index for *Lepus europaeus* in the study area

Variables	Marginality (4.4%)	FS1 (28.3%)	FS2 (12.9%)	FS3 (9.8%)
Altitude (m)	0.459	0.340	-0.203	0.426
Distance to the nearest road (m)	0.067	-0.008	0.021	0.036
Pasture-forest distance (m)	-0.400	0.326	0.503	0.036
Pasture-scrubland distance (m)	-0.209	-0.048	0.240	-0.240
Distance to the nearest pasture area (m)	-0.503	0.024	-0.714	-0.125
Grass area-forest distance (m)	-0.158	0.042	-0.065	-0.128
Grass area-scrubland distance (m)	0.023	0.114	-0.128	-0.129
Distance to the nearest grass area (m)	-0.174	-0.136	0.197	0.245
Distance to the nearest river (m)	-0.049	-0.051	-0.015	0.027
Distance to the nearest urban area (m)	0.018	0.065	-0.051	-0.044
Landscape patches density	0.088	-0.044	-0.039	0.073
Percentage of south orientation (%)	0.169	-0.009	-0.002	-0.024
Mean slope (%)	-0.153	0.074	0.024	0.009
Autumn rainfall (mm)	-0.077	0.152	0.126	0.440
Spring rainfall (mm)	0.017	-0.075	-0.100	-0.401
Winter solar radiation	0.159	0.002	-0.051	-0.111
Maximum summer temperature (°C)	0.003	0.835	-0.190	-0.152
Minimum winter temperature (°C)	-0.422	0.044	-0.093	0.501

Correlation between ENFA factors and the environmental descriptors is shown. FS are the specialisation factors. Percentages indicate the amount of specialisation accounted for by each factor

atory variables on parasite abundance and helminth richness by means of GLZ, respectively, using a Poisson error with a log link function (Wilson and Grenfell 1997) for abundance and a normal error with an identity link function for species richness. Standardisation was performed for all continuous explanatory variables in order to facilitate parameter comparisons.

We firstly modelled prevalence and abundance of different parasites and parasite richness, at species level, with all host-related variables taken into account in this study (Env+Pop+Ind). Afterwards, we modelled on the environmental and population variables simultaneously. By doing this, we obtained the amount of variation explained by both factor groups together (Env+Pop); in a similar way, we determined the amounts of variation explained by environment and individual together (Env+Ind), and by population and individual factors together (Pop+Ind). Then, the proportion of the variation explained exclusively by the environment (E) was obtained with the following subtraction: (Env+Pop+Ind)-(Pop+Ind). The proportions explained exclusively by population factors (P) and by individual factors (I) were obtained in a similar way. The amount of variation attributable exclusively to the interaction (or simultaneous influence) of environment and population factors (EP) was obtained with the subtraction (Env+Pop+Ind)-Ind-P-E. The amount of variation attributable exclusively to the interactions between environmental and individual factors (EI) and between population and individual factors (IP) was calculated in a

similar way. Finally, the amount attributable to the interactions between all three factors (EIP) was obtained with the subtraction (Env+Pop+Ind)-E-P-I-EP-IP-EI. Therefore, we provided a value for each part of deviance explained and knew how much corresponded to its pure effect and how much to interactions between groups of factors (Real et al. 2003; Carrete et al. 2007).

Results

Parasites

Hares were parasitized by ixodid ticks (*Rhipicephalus* spp., *Ixodes* spp., and *Haemaphysalis* spp.), hepatic trematodes (*Dicrocoelium dendriticum*), intestinal nematodes (*Trichostrongylus colubriformis*, *Trichostrongylus retortaeformis*, and *Trichuris leporis*), intestinal cestodes (Anoplocephalidae), and intestinal protozoa (*Eimeria* spp.). Parasite prevalence, mean abundance, and mean species richness found are shown in Table 2. Intestinal nematodes (mainly *Trichostrongylus* spp., 64%) and Coccidia (*Eimeria* spp., 71%) were highly prevalent; whereas, lower prevalence was found for the remaining parasites (not reaching one third of the sample, see Table 2).

Most (89%) European brown hares positive to *Trichostrongylus* sp. were exclusively infected with *T. retortaeformis*, and

Table 2 Sample size (n), parasite prevalence (percent), mean abundance, and mean species richness for different parasite taxa found in *Lepus europaeus*

		Number	Prevalence		Abundance	
			Percent	SD	Mean	SD
Ticks	All	64	31.250	0.473	5.143	5.710
	<i>Rhipicephalus</i> spp.	64	10.714	0.312	2.330	1.696
	<i>Ixodes ricinus</i>	64	17.857	0.386	9.000	6.344
	<i>Haemaphysalis</i> spp.	64	5.357	0.227	3.100	2.274
Trematodes	<i>Dicrocoelium dendriticum</i>	64	10.938	0.315	5.570	3.558
Nematodes	All	53	75.472	0.434	342.525	427.940
	<i>Trichostrongylus</i> spp.	53	64.151	0.482	400.529	431.033
	<i>Trichuris leporis</i>	53	24.528	0.434	8.000	4.755
Cestodes		53	33.962	140.778	0.478	41.390
Coccidia		53	71.698	63.429	0.455	101,833.300
Helminth richness		53	–	–	1.226	0.669
Species richness		42	–	–	2.286	1.065

the remaining 11% were co-infected with *T. retortaeformis* and *T. colubriformis*.

Habitat suitability model

Table 1 summarises the results of the ENFA analyses. The habitat suitability index obtained for *L. europaeus* is shown in Fig. 2. The marginality coefficient (which reflects the direction in which the species niche mostly differs from the available conditions in the study area) was 0.36, and the tolerance coefficient (the inverse of specialisation, which quantifies the acceptance to environmental factors of the species) was 0.57 (Hirzel et al. 2001). Explained information and explained specialisation of the habitat

suitability model were 77% and 55%, respectively. Eighteen descriptive variables were captured by four factors (the marginality factor and three specialisation factors) as shown in Table 1. The Jackknife validation method showed an $r_s=0.88$, confirming the predictive power of the resulting model.

Deviance partitioning

Deviance partitioning results of the prevalence, abundance, and parasite richness models for each parasite taxon are shown in Fig. 3. Overall, the average ED was 25.65% (range 4.27–76.27%). Higher values of ED were obtained for the abundance models (average ED=37.40%, range

Fig. 2 Habitat suitability map for European brown hare (*Lepus europaeus*) in the study area

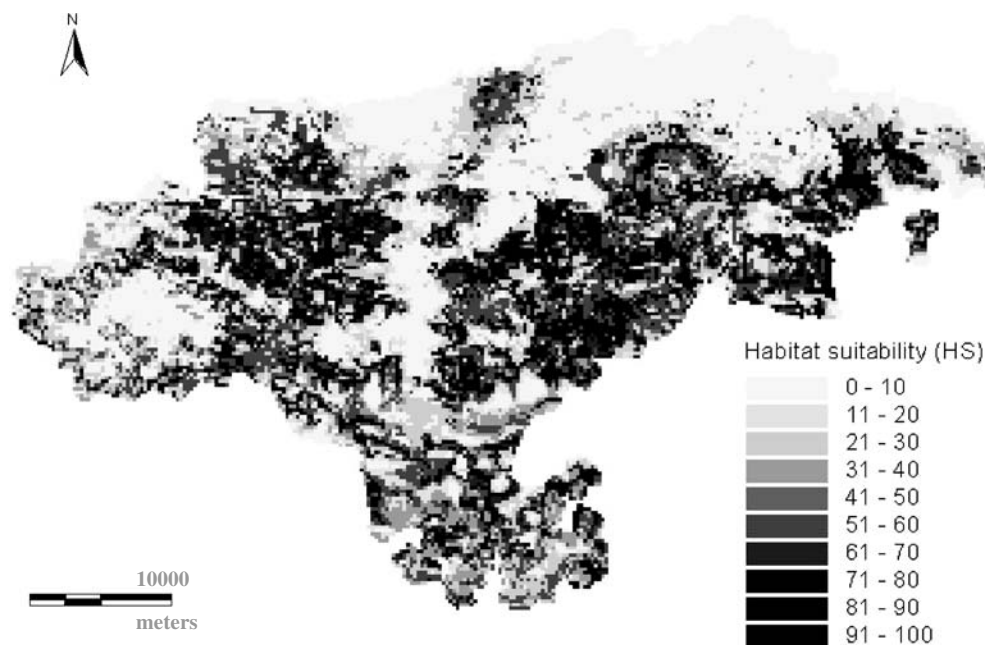
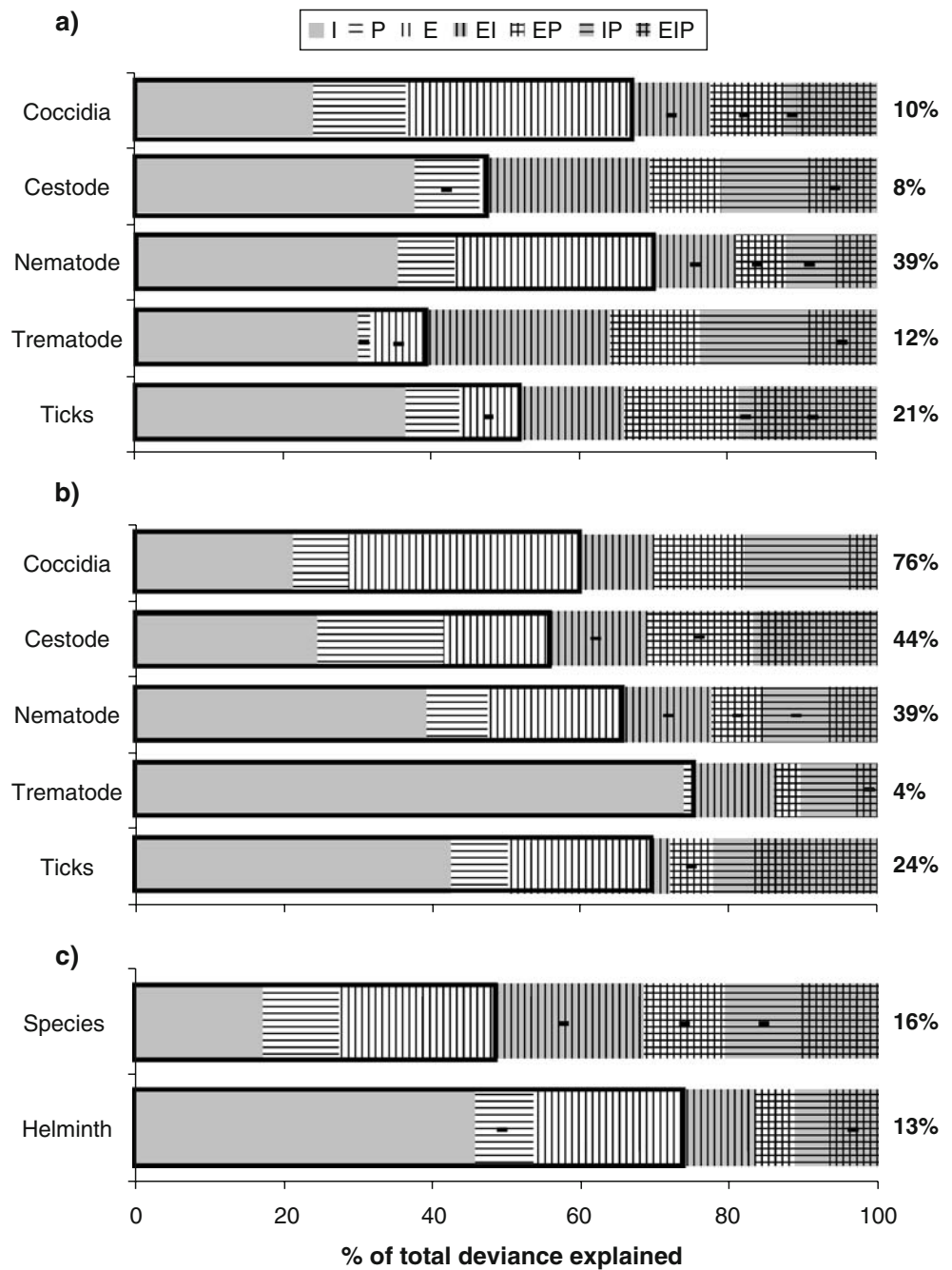


Fig. 3 Deviance partitioning results for each parasite group resulting from GLZ models (Statistica 6.0) in individual host (*I*), host environmental (*E*), and host population (*P*) factors and their interactions: **(a)** prevalence, **(b)** abundance, and **(c)** richness. The exclusive effects of the group factors (*I*, *P*, and *E*) are enclosed within a *thick line*. Percentage indicates total deviance explained by the maximal model. Negative deviances are also shown (–)



4.27–76.27%) than for the prevalence models (average ED=18.00%, range 7.69–39.36%; $\chi^2_{df=4}=99.75, p<0.001$). EDs for the prevalence models were followed by EDs for the richness models (average ED=14.75%, range 13.13–16.37%; $\chi^2_{df=1}=4.86, p=0.027$). Individual factors group explained the largest proportion of the ED in the different models (average ED=35.81%, range 0.51–38.48%). This group was followed in relevance by the environmental factors (average=16.39%, range 0.02–24.98%; $\chi^2_{df=15}=996.33, p<0.001$). Environmental factors explained more deviance than the environment-individual interaction (average=

13.50%, range 0.38–18.65%; $\chi^2_{df=15}=127.14, p<0.001$). This hierarchy was similar for the prevalence, abundance, and species richness models (Fig. 3). In contrast, population factors (i.e., hare abundance) had a low relevance in explaining deviance of the different models (average=8.05%, range 1.17–16.85%).

Models for parasites with a direct life cycle yielded higher ED values (average ED=35.10%, 14.70%, and 43.02%, for prevalence, abundance, and species richness, respectively) than those for indirect life cycle ones (average ED=16.93%, 9.89%, and 23.98%, for prevalence, abun-

dance, and species richness, respectively; $\chi^2_{df=3}=143.34$, $p<0.001$; see Fig. 4). Individual factors were the most relevant group of explanatory variables for both types of parasites (34.40% and 35.42% of total ED for direct and indirect life-cycle parasites, respectively, see Fig. 4, no statistical difference was evidenced). Environmental factors were more relevant in models for direct life-cycle parasites (21.00% of total ED, $\chi^2_{df=1}=24.57$, $p=0.021$). Population factors explained only 8.40% and 9.07% of the total ED in direct life-cycle and indirect life-cycle parasites, respectively (no statistical difference was evidenced). In prevalence models for indirect life-cycle parasites, individual factors were followed in relevance by environment-individual factors (23.51% of total ED) and by population factors in abundance models (13.00%, see Fig. 4).

Exceptionally, in the case of coccidia models, environmental factors explained higher percentages of deviance than individual factors (30.24% and 31.44% for prevalence and abundance models, respectively), contrasting with results on the other direct life-cycle parasites (see Fig. 3).

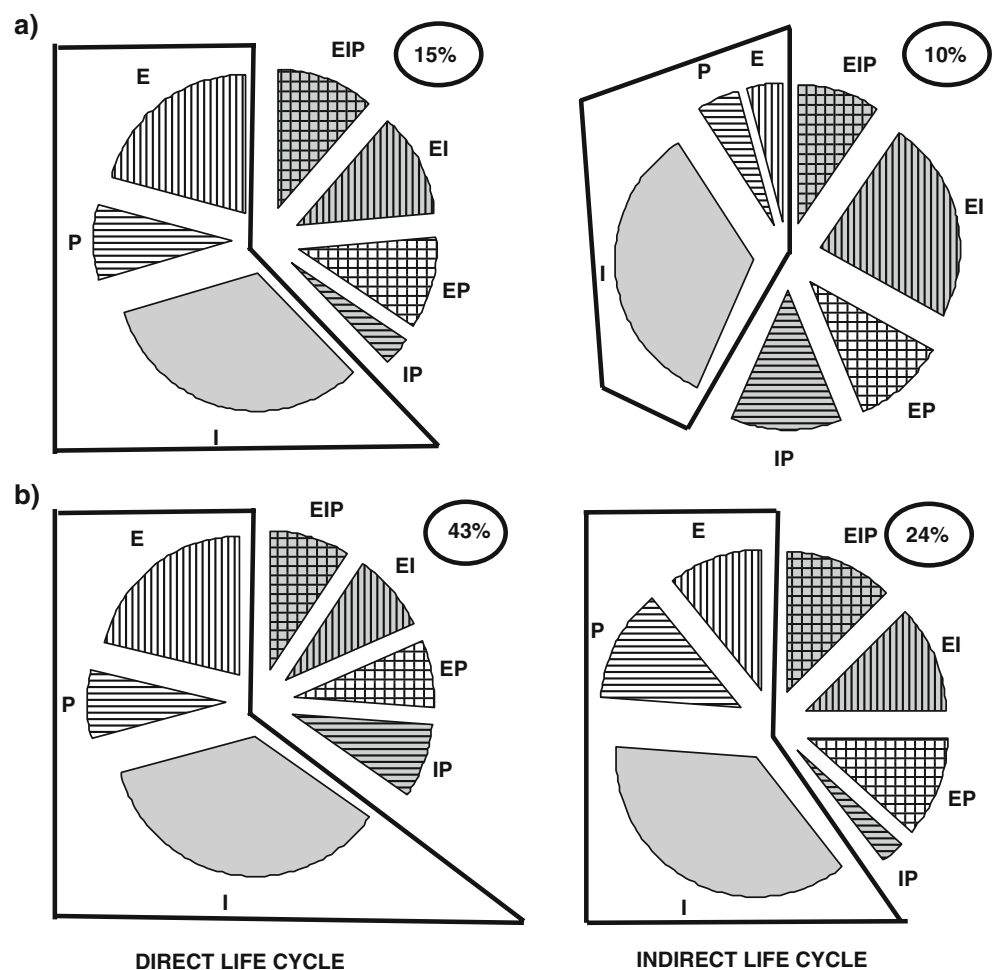
Discussion

Applicability

We provided a practical means to study the relative contribution of host-related sources of variation to parasitization. This methodology had been used to explain the distribution of free-living species (e.g., Real et al. 2003; Heikkinen et al. 2005) but not to study parasitization patterns (Barbosa et al. 2005). This global perspective allowed (1) interpreting individual parasitization in the context of host life traits and host environmental variation; and (2) using parasites as bio-indicators of host condition or environmental suitability (Hogue and Swig 2007), with a sound ecological support.

Traditional methods to explore the importance of different factors in determining the prevalence, abundance, and species richness of parasites in their hosts have been limited to assess only a small number of potential variables. Here, we presented a novel application of deviance partitioning to explore the relative contribution of three

Fig. 4 Deviance partitioning for each parasite life-cycle type (direct or indirect) calculated as the average deviance resulting from single parasite models. Partitioning was achieved in individual (*I*), host environmental (*E*), and host population (*P*) factors and their interactions: (a) prevalence and (b) abundance. The exclusive effects of the group factors (*I*, *P*, and *E*) are enclosed within a *thick line*. Percentages indicate average deviances explained by the maximal models



levels of factors on the prevalence, abundance, and species richness of a range of parasites of the European brown hare. In spite that this study was based on a limited number of animals, we showed the applicability of deviance partitioning to assess the factors driving parasitization in a given host and study area. In view of the emergence of the environmental health, deviance partitioning may help to analyse data on emergent diseases, or which factors are more relevant for zoonotic diseases or in endangered host species. Limitations, from a methodological point of view, may also arise when analyses do not include some relevant factors, and the actual relative contribution of the different sources of variation in parasitization becomes unknown. Our analyses focused on host-related source of variability and did not include other factors, such as those not host-related, which could determine that the percentage of deviance explained in these models is not an absolute value but a percentage within the host-related factor. Secondly, the omission of influential factors may be reducing the explanatory power of the models. Nonetheless, by using deviance partitioning, we are able to quantify the proportion of the deviance which was not explained by the selected factors and, hence, we assumed it to be explained by uncontrolled factors.

Seasonal pattern of parasitization was not studied because it was not the aim of this research so we reduced the sampling period to one specific season (autumn).

Deviance partitioning: general patterns

The relevance of individual factors we found may underline that they are more relevant respect to the other we tested (host population and host environment). First, host characteristics such as space use (Bordes et al. 2009), or behaviour, which is commonly dependent on factors such as age, sex, reproductive and social status, and their interactions (reviewed by Wilson et al. 2002), can influence the exposure to parasites. Second, the ability to mount an effective immune response during and after exposure is another key individual factor modulating parasite establishment and abundance (Möller et al. 1998). Therefore, host body condition, which determines resources available to immunity, may play a relevant role as individual factor (e.g., Vicente et al. 2007b; Alzaga et al. 2008). Particularly, immune traits may interact with population and environment factors (see discussion below).

Parasites depend on two environments: one reflecting external conditions, the other created by the living host (Thomas et al. 2004). The fact that the models on abundance better describe parasitization can be due to the parasite load-dependent properties of host-parasite interaction evidenced (Anderson and May 1978). For prevalence models in which the ED is low, variables not included in

the model (non host-related factors or parasite immediate environment) may be playing an important role in driving host-parasite relationships. Nonetheless, models based on parasite prevalence on hosts could add very valuable information to abundance models, for example, to elucidate factors limiting parasite persistence in populations and environments. Clearly, more research is needed on these factors and their interaction with host individual traits and the environment. Also, the epidemiological differences between micro- and macroparasites make it interesting facing future studies on the issue.

Host individual factors were followed in relevance by host environmental factors and their interaction. Host environmental factors can modulate parasite abundance in several non-mutually exclusive ways. First directly, by influencing free-living stage viability or transmission, and second indirectly, by mediating effects on hosts. A low habitat suitability could negatively affect host fitness (Franklin et al. 2000; Carbonell et al. 2003) and, hence, the adult parasite's habitat. Chronic stress experienced by hosts has often been associated to increased parasite loads (Villanúa et al. 2006). Therefore, inappropriate environmental conditions for hares can be considered a possible source of stress (van Oort and Otter 2005), for example, adverse climatic conditions, low food availability, scarcity of shelter areas, or human encroachment into hare habitats. Additionally, hares may also avoid habitats where exposure to parasites is higher (Hutchings et al. 2002).

Deviance partitioning: parasite traits

As predicted, the relative importance of host individual factors and host external environment varied according to the nature and life cycle strategy of the parasite (Tinsley 2005). Our results suggested that environmental factors had an increased influence on direct life-cycle parasite infection rates. One would expect the opposite pattern that the environment has more influence on indirect life-cycle parasite as long they have a more complex cycle that can be more influenced by environmental variables. One possible explanation for this general trend is that indirect life-cycle parasites develop transmission strategies able to avoid abiotic environment constraints but ensure transmission to intermediate hosts. Some relationship between habitat suitability for the host and for the free-living stages of parasites could be explaining the environmental influence on direct life-cycle parasites.

Our results also suggested that host population factors (host abundance) had an increased influence on indirect life-cycle parasite infection rates, evidencing density-dependent parasite transmission. We cannot discard that high host abundance may correlate with increased chances for intermediate hosts to become infected (environmental

presence of excretion propagules may increase as the number of excreting hares and host susceptibility to infection does). Probably, to evidence host density-dependent effects on parasite spread and distribution through hares, a wider range of hare abundances than we found is needed (Arneberg 2002; Acevedo et al. 2005).

In summary, while taking into account the study limitations, we suggest that parasitization can be used not only as an indicator of individual fitness but also as an indicator of environmental quality for the host. This research also underlines the importance of monitoring parasite rates together with environmental, population, and host factors. Deviance partitioning can provide new insights of broad scale elements affecting host-pathogen interactions in wildlife, even in the context of global change.

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