Temporal dynamics of direct reciprocal and indirect effects in a host–parasite network

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Summary

1. Temporal variation in the direct and indirect influence that hosts and parasites exert on each other is still poorly understood. However, variation in species' influence due to species and interactions turnover can have important consequences for host community dynamics and/or for parasite transmission dynamics, and eventually for the risk of zoonotic diseases.
2. We used data on a network of small mammals and their ectoparasites surveyed over 6 years to test hypotheses exploring (i) the temporal variability in direct and indirect influences species exert on each other in a community, and (ii) the differences in temporal variability of direct/indirect influences between temporally persistent (TP) and temporally intermittent species.
3. We modelled the temporal variation in (i) direct reciprocal influence between hosts and parasites (hosts providing resources to parasites and parasites exploiting the resources of hosts), using an asymmetry index, and (ii) indirect influence among species within a community (e.g. facilitation of parasite infestation by other parasites), using betweenness centrality. We also correlated asymmetry and centrality to examine the relationship between them.
4. Network dynamics was determined by TP species but even those species had strong among-species heterogeneity in the temporal variation of the direct/indirect effects they exerted. In addition, there was a significant positive linear correlation between asymmetry and centrality.
5. We conclude that the temporal dynamics of host–parasite interactions is driven by TP hosts. However, even within this group of persistent species, some exhibit large temporal variation, such that the functional roles they play (e.g. in promoting parasite transmission) change over time. In addition, parasites having a large negative impact on hosts are also those facilitating the spread of other parasites through the entire host community. Our results provide new insights into community dynamics and can be applied in the management of antagonistic networks aimed at preventing disease outbreaks.

Key-words: antagonistic interactions, antagonistic networks, community ecology, disease ecology, ecological networks, fleas, generalized least-squares models, host–parasite interactions, mites, network analysis

Introduction

The temporal dynamics of host–parasite interactions has been a major theme in evolutionary and disease ecology, especially in the context of diseases spread within a population. Traditional approaches address the rate at which a given parasite (or pathogen) invades a population of a given host (Anderson & May 1991). However, host species usually harbour more than one parasite species, while the majority of parasite species can exploit more than one host species, with the resulting interactions being

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extremely complex (Vázquez *et al.* 2005, 2007; Ezenwa & Jolles 2011). Consequently, recent studies have started to aim to understand host–parasite interactions at a community scale (Begon 2008; Rohani *et al.* 2008), but these studies usually examine each of the communities separately without considering the added dimension of time.

A complex system of host–parasite interactions can be depicted as a bipartite network where nodes represent species and in which nodes from one set (e.g. hosts) are allowed to interact only with nodes of the other set (e.g. parasites) (Vázquez *et al.* 2005). Despite considerable research efforts on such antagonistic bipartite networks, very few studies address their dynamic aspect. One study of a host–parasitoid network has shown that the structure of the host and parasitoid communities changes over time and that the dynamics is affected by human activities (Laliberté & Tylianakis 2010). Here, we address an additional aspect and explore the temporal dynamics of species' functional roles. This topic has never been studied, despite the profound ecological consequences of host–parasite dynamics to host and parasite populations or communities (Hudson, Dobson & Newborn 1998; Beldomenico *et al.* 2008).

The interdependency of species in a network creates a wealth of pathways by which species can influence each other. Direct reciprocal influence can be defined as the positive effect of a host on a parasite (e.g. providing it with resources) and the negative effect of a parasite on a host (e.g. exploiting its resources). For simplicity, we refer to this influence as a direct effect. In a host–parasite network, direct effects can be captured by using indices of interaction asymmetry estimated via relative abundances, reflecting the overall direct influence of a focal species on other species with which it interacts (Vázquez *et al.* 2007). In particular, parasite i would have a direct strong influence on its host j if its abundance on that particular host is high relative to the abundance of all other parasites infesting the host. Similarly, a host j would have a direct strong influence on a parasite i if the parasite's abundance is high in that particular host, relative to the parasite's abundance on all the other hosts it infests. When the influence of parasite i on host j is stronger/weaker than the influence of host j on parasite i, the nature of the interactions between i and j is considered asymmetric (Vázquez *et al.* 2007). This definition of direct effects assumes a negative linear relationship between parasite abundance and host fitness and an equal effect of parasites on hosts. Although these assumptions are somewhat limiting (see Discussion), they are rooted in true biological processes (Lehmann 1993). For example, studies on small mammals demonstrated negative relationships between parasite loads and host fitness (Arnold & Anja 1993; Van Vuren 1996; Neuhaus 2003; Hawlena, Abramsky & Krasnov 2006).

Indirect influence is considered within each community. By indirect influence, we mean the negative role that a host species plays in contributing to infestation of other host species by parasites and the positive role a parasite species has in facilitating the infestation of a host by other species of parasites (Krasnov *et al.* 2005). Hosts infested by many parasite species can propagate horizontal transmission of parasites across the network to other hosts and thus serve as reservoirs of parasites. A parasite species can facilitate the infestation of other parasite species by, for example, initiating a primary immune response, lowering the defence threshold of the host and making it more susceptible to attacks by other parasites (Krasnov *et al.* 2005; Leung & Poulin 2007). A recent study on apparent competition in a host–parasitoid network has clearly shown that the experimental removal of specific hosts indirectly reduced parasitism of other hosts that are attacked by parasitoids of the removed species (Morris, Lewis & Godfray 2004).

One way of capturing indirect effects is by using centrality measures, which indicate the relative importance of a node in a network (Freeman 1979). Detecting central nodes has been a major issue in social network research, but less so in ecological networks (e.g. Fortuna *et al.* 2009; Martín González, Dalsgaard & Olesen 2010; Anderson & Sukhdeo 2011). In social sciences, centrality measures quantify a focal node's potential in mediating the transmission of information. In individual-based host networks, host centrality is positively correlated with efficiency of parasite transmission (Fortuna *et al.* 2009; Salathé *et al.* 2010). In food webs, host centrality was a consistent predictor of parasite diversity of a host species (Anderson & Sukhdeo 2011). Thus, in a host–parasite network, a central host species potentially transmits parasites to many other host species, and a central parasite species potentially facilitates the establishment of other parasite species in/on a host. The centrality of a node depends not only on its traits (e.g. host specificity of a parasite), but also on the availability and behaviour of other nodes in the network (Freeman 1979). This is important in the context of this study because the centrality of a focal node may vary if the availability of other nodes varies over time.

Examining the temporal dynamics of species' asymmetry and centrality in host–parasite networks is crucial for a better understanding of the dynamics of the propagation of a parasite or a pathogen throughout the network, which has applied consequences. For example, from a population dynamics perspective, strong temporal variation in host–parasite interactions may affect the regulation of host populations by parasites (Hudson, Dobson & Newborn 1998). Here, we use data from a 6-year survey of small mammals and their arthropod ectoparasites (fleas and gamasid mites) to investigate the temporal dynamics of species' direct and indirect influences at species and community levels.

Recent studies have shown that community composition is dynamic, with some species/interactions occurring in certain years, but not in others (Olesen, Stefanescu & Traveset 2011). We explore this phenomenon in our study

system. Due to the variability among species within a community in their patterns of interactions (Olesen, Stefanescu & Traveset 2011; Poisot *et al.* 2012), we hypothesized (H1) that temporal variability in direct and indirect influences would differ across species within a community. This hypothesis is not at all obvious because if, due to the high intimacy characteristic to host–parasite interactions, the associations between hosts and parasites are maintained across years, then temporal variability in species influence will be homogenous across species within a community. We examined this hypothesis by focusing on species that persisted in the system throughout the 6 years (hereafter, core species). Core species persist in the system, but their interactions with other species may be dynamic (Olesen, Stefanescu & Traveset 2011; Poisot *et al.* 2012).

In order to take into account the fact that some species were more temporally persistent (TP) in the system than others, we defined species that occurred in the network for >2 years (not necessarily consecutive) as TP or otherwise as temporally intermittent (TI). We examined the hypothesis (H2) that the TP and TI species would differ in their temporal variability of direct/indirect influence because intermittent species have fewer opportunities to interact with other species. Finally, we tested the relationship between asymmetry and centrality by correlating them at the species level within each community. A positive correlation would indicate that species that exert more direct influence also have a greater indirect influence.

Materials and methods

DATA SET

We used a comprehensive data set on fleas and gamasid mites collected from the bodies of small mammalian hosts in the vicinity of the city of Novosibirsk (Russia; 54°51′16·92″N, 83°6′24·48″ E) during a 6-year (1982–1987) survey (Krasnov *et al.* 2010). Fleas are obligate haematophagous ectoparasites most abundant and diverse on small- and medium-sized mammals. In most fleas, all stages of the life cycle are spent off the host, except for the adults that feed intermittently on the host, while spending the rest of lives in a burrow or nest of a host. The mites included in our networks were both facultative and obligatory haemato- and/or lymphophages. These mites use their hosts both as food sources and as dispersal vehicles, and thus, the association between these mite species and their hosts is assumed to be very intimate (Radovsky 1985). As is the case for fleas, gamasid mites spend much time in hosts' burrows. Transmission of fleas and mites from host to host is usually achieved via visiting each other's burrows, although transmission via direct between-host contacts (Krasnov & Khokhlova 2001) and free active or passive dispersal (Vinarski *et al.* 2007) cannot be ruled out.

Our analyses were limited to host species for which at least 10 individuals were captured. To remove any possible effect of sampling contamination or accidental host–parasite associations, only host–parasite associations in which a host species harboured $\geq$ 5% of all individuals of a parasite species were used (Dick 2007). Prior to main analyses, the sampling effort in each year was estimated using species accumulation curves. The curves showed that the trapping sessions each year were sufficient to detect all host species present in the community in that year (see Appendix S1, Supporting information). This allowed us to assume that the sampling effort was equal among the years.

For each yearly survey, a matrix with rows representing host species and columns representing parasite species was constructed (see Data accessibility). The strength of an interaction between a parasite and a host was measured via the mean abundance of a parasite species on a host species (i.e. the mean number of parasites of a given species per individual of a given host species). The matrix cell values thus represented the interaction strength between any pair of interacting species. Abundance values were rounded to the nearest integer. When mean abundance was <0·5, we set a value of 1.

NETWORK ANALYSIS

Species turnover and network connectance

The yearly turnover of species and interactions was calculated following Olesen, Stefanescu & Traveset (2011). The mean annual species/interaction turnover t was calculated as $(e/(e + s) + c/(c + s))/2$, where e was the number of extinctions (the species/interaction appeared in year y, but not in year $y + 1$), c was the number of colonizations (did not appear in year y, but appeared in year $y + 1$), and s was the number of survivals (appeared in both years y and $y + 1$) for a given species/interaction. To evaluate the general structure of the whole network, the network connectance was calculated as the number of realized interactions divided by the maximum possible number of interactions in each year.

Interaction asymmetry

To evaluate the asymmetry in interactions of each species in each of the yearly subnetworks, we used the asymmetry index Ai of Vázquez *et al.* (2007). In brief, the direct influence of parasite i on host j (S_{ij}) is subtracted from the influence of host j on parasite i (S_{ji}), where S_{ij} is the interaction strength of parasite i and host j, relative to the interaction strengths of all other parasites infesting host j. Similarly, S_{ji} is the interaction strength of host j and parasite i, relative to the interaction strengths of all other hosts infested by parasite i. The Ai of a species i is calculated as $\left[\sum_{j=1}^{J} (S_{ij} - S_{ji})\right]/k_i$, where k_i is the number of interactions of species i. The index ranges between −1 and 1, where −1 indicates that the focal species is strongly affected by its interaction partners (influenced), and 1 indicates that it exerts a strong effect on them (influential).

Species centrality

We measured centrality using betweenness centrality (BC), which quantifies the extent to which a focal node lies on the shortest paths between two other nodes. In biological terms, BC indicates how efficient a host species is in serving as a mediator for the transmission of parasites across hosts and how efficient a parasite is in facilitating the transmission of parasites across hosts. This interpretation makes BC very informative for our purposes and we thus focused on it rather than on other indices of centrality. To calculate BC, the bipartite network was projected into two unipartite networks, connecting two nodes from the same set

(e.g. parasite species) if they shared at least one node from the other set (e.g. host species). Fortuna *et al.* (2009) used centrality indices in projected networks and showed a positive correlation between centrality and pathogen transmission. A similar approach was taken by Morris, Lewis & Godfray (2004), who examined apparent facilitation among hosts based on shared parasitoids. Betweenness centrality was rescaled by dividing it by the maximal index value. Rescaled BC values ranged from 0 to 1, where 1 represents the highest centrality score in a particular network. This aided in the comparison of the importance of different host/parasite species across years.

STATISTICAL ANALYSES

Across species within a community, temporal variation in Ai and BC can be either homogeneous or heterogeneous. When temporal variation is heterogeneous, the value of Ai or BC varies greatly across years in some species, while very little in others. Such heterogeneity would point to differences among host or parasite species in the temporal dynamics of interactions with species from the opposite group. Our approach was to compare a statistical model in which the variance component of the fixed factor *species* was homogeneous (hereafter, a *homoscedastic* model) to a model where it was heterogeneous (hereafter, a *heteroscedastic* model). The homoscedastic models were mixed-effects linear models with year as a random factor and a homogeneous variance component, whereby all factor levels (i.e. species) had equal across-year variance (Zuur *et al.* 2009). Year was set as a random factor instead of a fixed continuous variable because we were not interested in quantifying a trend in either Ai or BC over time (i.e. we were not interested in a constant increase or decrease), but rather in its net variation. The counterpart heteroscedastic models were mixed-effects generalized least-squares models, essentially identical to the homoscedastic models, except they had a heterogeneous variance component, allowing each species to have a different across-year variance (Zuur *et al.* 2009). In each homoscedastic–heteroscedastic model pair (Table 1), a better fit of the heteroscedastic model to the data would mean that there are differences among species in the temporal variation of the index. Model pairs were compared with Akaike Information Criterion (AIC) (the lower the AIC, the better the model). A difference of >2 AIC was regarded as a threshold to discard one of the models. Note that temporal variation can be large in the homoscedastic model, albeit equal among species. It can be argued that values of Ai or BC of a certain species would be more similar in consequent years. This will be manifested as an autocorrelation between consecutive model residuals. We visually tested for autocorrelation in the data using acf plots depicting the empirical autocorrelation function for the within-group residuals from a model fit (Pinheiro & Bates 2000). We found no evidence for autocorrelation in all models.

To test the hypothesis that temporal variability in direct and indirect influences would differ across species within a community (H1), the effect of the identity of core species on Ai and BC was examined within both communities using four model pairs (model pairs 1–4, Table 1). The models also allowed us to determine whether a species' yearly-average Ai and BC indices differed significantly from zero. A zero value of Ai indicates that, on average, there is symmetry in the direct influence between a species and the species with which it interacts. A zero value of BC for a focal species means that there are no shortest paths between any

Table 1. List of model pairs used in the analyses. Each pair consisted of two mixed-effects generalized least-squares models with year as a random factor, where one of the models had a homogenous variance component (Hm) and the other a heterogeneous variance component (Ht). In the heteroscedastic models, each species (denoted by j) or persistence level (denoted by k) was allowed to have different variance. The best model of each pair was selected by Akaike Information Criterion (AIC)

Model	Variance structure Hm/Ht	AIC (Hm/Ht)
Fixed factor species[a]		
1 Ai ~ Host species	$N(0, \sigma^2)/N(0, \sigma_j^2)$	35/5
2 Ai ~ Parasite species	$N(0, \sigma^2)/N(0, \sigma_j^2)$	−3/−81
3 BC ~ Host species	$N(0, \sigma^2)/N(0, \sigma_j^2)$	43/24
4 BC ~ Parasite species	$N(0, \sigma^2)/N(0, \sigma_j^2)$	32/−179
Fixed factor persistence[b]		
5 Ai ~ Host persistence	$N(0, \sigma^2)/N(0, \sigma_k^2)$	63·5/64·4
6 Ai ~ Parasite persistence	$N(0, \sigma^2)/N(0, \sigma_k^2)$	202·1/203·5
7 BC ~ Host persistence	$N(0, \sigma^2)/N(0, \sigma_k^2)$	61/19
8 BC ~ Parasite persistence	$N(0, \sigma^2)/N(0, \sigma_k^2)$	41/2

[a]Models were run with host/parasite species that persisted for 6 years.
[b]Models were run on all species within the host/parasite community.

two nodes that pass through the focal node, and thus, its role can be defined as 'peripheral'. Otherwise, it can be defined as a 'connector' (Martín González, Dalsgaard & Olesen 2010).

To test the hypothesis that TP and TI species would differ in their temporal variability of direct/indirect influence (H2), all the species within each community were used. We followed the same modelling procedure we used to test H1 and tested for differences in asymmetry and centrality between TP and TI species within a community. Therefore, the fixed factor was *persistence* (rather than species) with two levels: TI and TP (model pairs 5–8, Table 1). Heterogeneous temporal variation would indicate that TP and TI species differ in the dynamics of their influence in the network and would thus point to differences in the roles they play in network formation. A significant effect of persistence in either model would indicate that, on average, TP and TI species differ in the direct or indirect influence they exert.

Finally, to understand the relationship between asymmetry and centrality at the species level within each community, we correlated Ai and BC using Pearson's correlation. A positive correlation would indicate that species that exert more direct influence also have a greater indirect influence. We included only the core species in this analysis.

Analyses were done in R version 2.15 (R Development Core Team 2012) using the bipartite (version 1.18; Dormann *et al.* 2009) and nlme (version 3.1-106; Pinheiro *et al.* 2012) packages. We provide an R code with all the analytical procedures in Appendix S2, Supporting information.

Results

Across six years, the network comprised 21 host and 71 ectoparasite species (54 mite species and 17 flea species; Table S1, Supporting information). In the yearly networks of 1984, 1985 and 1987, there were no TI hosts, and in

the yearly network of 1987, there were no TI parasites. Eighty-one per cent of hosts were TP (occurred in more than 2 years), but only 52% occurred in all 6 years. Sixty-eight per cent of parasite species were TP, but only 24% of parasites occurred in all 6 years (11 mites, 6 fleas) (Table S1 and Figs S1 and S2, Supporting information). Across years, only 265 interactions were realized at least once, out of 1491 (21 hosts × 71 parasites) possible ones. In other words, the connectance of the network aggregated across the years was 17·8% (=265/1491). The yearly networks were smaller, but their connectance remained roughly the same (14·9–21·6%).

SPECIES AND INTERACTION TURNOVER

Host turnover rate ranged from 0 to 1 with a mean ± SD of 0·29 ± 0·4 and a median of 0. Mean parasite turnover was 0·43 ± 0·4, with a median of 0·25. Interaction turnover was high, with 40% of the realized interactions appearing in 1 year only (Fig. S2, Supporting information).

HYPOTHESIS H1: TEMPORAL DYNAMICS OF CORE SPECIES

In across-species analyses of asymmetry, the fit of the heteroscedastic model to the data was better than that of the homoscedastic model for core hosts and parasites (model pairs 1–2, Table 1). Thus, within each community, the coefficient estimates of the variance in A_i were small (close to zero) for some species but large for others, indicating that the direct influence of only some of the species within a community was variable across years (Fig. 1a, b). In 45% of core hosts, the yearly-averaged A_i estimated by the model was significantly greater than zero, and in one case (a vole *Myodes rufocanus*), it was significantly lower than zero (Table 2; see Fig. S3, Supporting information, for the raw values of asymmetry for hosts). In parasites, yearly-averaged A_i estimated by the model was significantly lower than zero in 71% of core species and, in no case, it was higher than zero (Table 2; see Fig. S4, Supporting information, for the raw values of asymmetry for parasites).
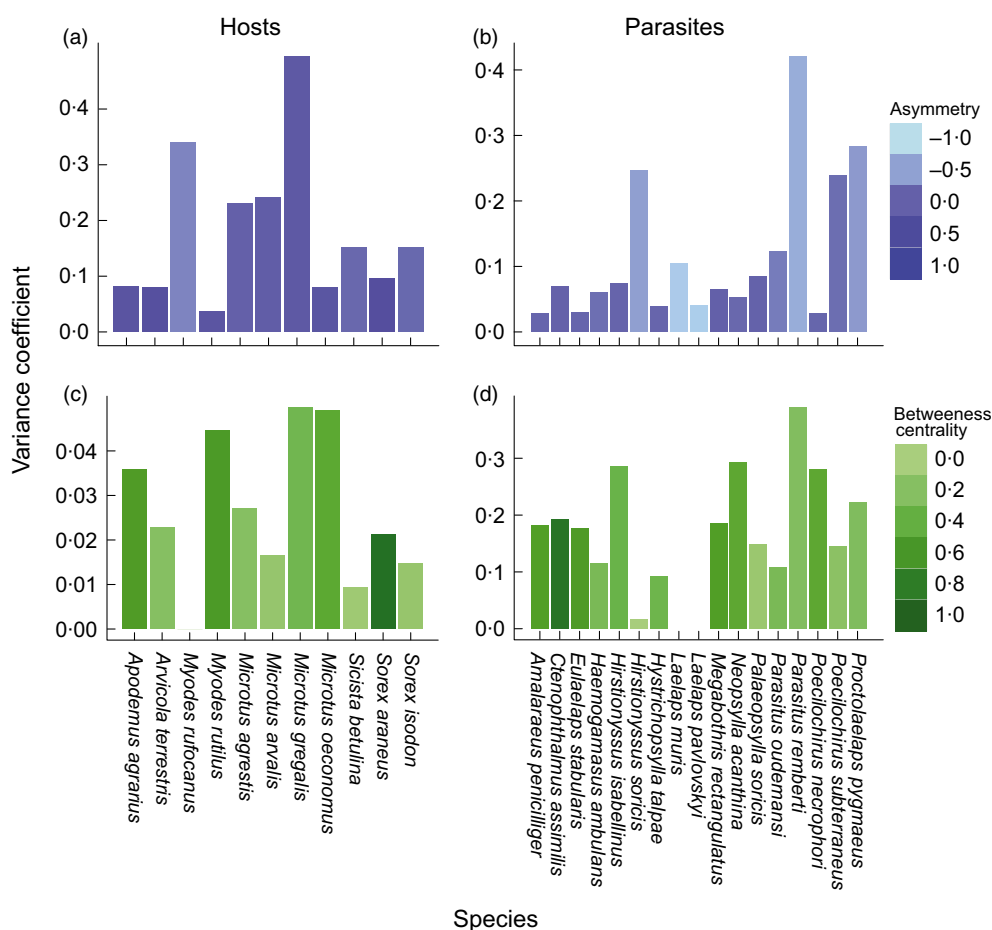
Fig. 1. Within-species temporal variation in asymmetry (a, b) and rescaled betweenness centrality (c, d) for hosts and parasites. Temporal variation is represented by the value of the variance coefficient (height of bars) estimated from a mixed-effects generalized least-squares model with year as a random factor and a heterogeneous variance component, allowing each species to have different across-year variance. Palettes a-d correspond to models 1–4, respectively (see Table 1). Shade (colour in the online version) strength indicates how asymmetric (a, b) or central (c, d) a species is, based on model estimates. Only 11 host and 17 parasite species that occurred in the network for 6 years are included. Species are ordered alphabetically.

Table 2. Estimation of coefficients (± SE) of asymmetry (Ai) and rescaled betweenness centrality (BC) by a mixed-effects generalized least-squares model with year as a random factor and heterogeneous variance component, allowing each host species to have a different across-year variance. Only 11 host and 17 parasite species that occurred in the network for 6 years were included. The results correspond to the heteroscedastic models of pairs 1–4 in Table 1

Species	Ai			Rescaled BC		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
Hosts						
Apodemus agrarius	0·223 (0·033)	6·75	**0**	0·555 (0·11)	5·037	**0**
Arvicola terrestris	0·3 (0·033)	9·13	**0**	0·197 (0·072)	2·754	**0·008**
Myodes rufocanus	−0·299 (0·139)	−2·15	**0·036**	0·035 (0·018)	1·961	0·055
Myodes rutilus	0·186 (0·015)	12·40	**0**	0·572 (0·137)	4·176	**0**
Microtus agrestis	0 (0·094)	0·00	0·998	0·2 (0·084)	2·376	**0·02**
Microtus arvalis	0·044 (0·098)	0·45	0·656	0·103 (0·053)	1·968	0·055
Microtus gregalis	0·116 (0·202)	0·57	0·569	0·331 (0·152)	2·17	**0·035**
Microtus oeconomus	0·179 (0·033)	5·48	**0**	0·445 (0·15)	2·965	**0·005**
Sicista betulina	−0·087 (0·062)	−1·40	0·169	0·056 (0·033)	1·662	0·103
Sorex araneus	0·341 (0·04)	8·63	**0**	0·891 (0·067)	13·341	**0**
Sorex isodon	−0·098 (0·062)	−1·59	0·118	0·101 (0·048)	2·096	**0·04**
Parasites – fleas						
Amalaraeus penicilliger	−0·055 (0·013)	−4·26	**0**	0·518 (0·074)	6·983	**0**
Ctenophthalmus assimilis	−0·02 (0·029)	−0·68	0·498	0·86 (0·078)	10·979	**0**
Hystrichopsylla talpae	−0·064 (0·017)	−3·83	**0**	0·347 (0·038)	9·196	**0**
Megabothris rectangulatus	0·008 (0·027)	0·30	0·766	0·536 (0·076)	7·061	**0**
Neopsylla acanthina	−0·092 (0·023)	−4·07	**0**	0·45 (0·119)	3·773	**0**
Palaeopsylla soricis	−0·01 (0·035)	−0·28	0·777	0·073 (0·06)	1·206	0·23
Parasites – mites						
Eulaelaps stabularis	−0·059 (0·013)	−4·38	**0**	0·562 (0·073)	7·754	**0**
Haemogamasus ambulans	−0·134 (0·025)	−5·35	**0**	0·287 (0·047)	6·098	**0**
Hirstionyssus isabellinus	−0·04 (0·031)	−1·30	0·196	0·368 (0·117)	3·141	**0·002**
Hirstionyssus soricis	−0·482 (0·101)	−4·78	**0**	0·006 (0·005)	1·195	0·24
Laelaps muris	−0·827 (0·043)	−19·24	**0**	0 (0)	1·574	0·12
Laelaps pavlovskyi	−0·87 (0·018)	−49·56	**0**	0 (0)	1·579	0·12
Parasitus oudemansi	−0·248 (0·05)	−4·93	**0**	0·285 (0·044)	6·478	**0**
Parasitus remberti	−0·584 (0·172)	−3·40	**0·001**	0·226 (0·159)	1·42	0·16
Poecilochirus necrophori	−0·074 (0·013)	−5·85	**0**	0·457 (0·115)	3·98	**0**
Poecilochirus subterraneus	−0·132 (0·097)	−1·36	0·178	0·167 (0·059)	2·827	**0·006**
Proctolaelaps pygmaeus	−0·436 (0·116)	−3·76	**0**	0·234 (0·091)	2·587	**0·011**

Coefficients significantly different than zero are in boldface.

For core host species, the fit of the heteroscedastic model to the data was better than that of the homoscedastic model for BC (model pair 3, Table 1). Temporal variation in BC was therefore unequal across host species (Fig. 1c). Furthermore, the three host species with the lowest variation were also characterized by the lowest BC across years (a vole *Myodes rufocanus*, a birch mouse *Sicista betulina* and a shrew *Sorex isodon*; Fig. 1c; see Fig. S5, Supporting information, for the raw BC values of hosts). The BC model showed that 73% of hosts had a yearly-averaged BC significantly larger than zero (Table 2). The results of the model point to a woodmouse *Apodemus agrarius*, voles *Myodes rutilus* and *Microtus oeconomus* and a shrew *Sorex araneus* as the most central hosts across years, despite their considerable temporal variation in BC (Fig. 1c).

For core parasite species, the fit of the heteroscedastic model to the data was better than that of the homoscedastic model for BC (model pair 4, Table 1). Therefore, ectoparasites differed in their degree of the temporal variation in BC (Fig. 1d). The model revealed that 71% of

core ectoparasites had a BC significantly greater than 0 (Table 2; see Fig. S6, Supporting information, for the raw BC values of parasites).

HYPOTHESIS H2: TEMPORAL DYNAMICS OF TEMPORALLY PERSISTENT AND INTERMITTENT SPECIES

When examining differences in Ai between TP and TI host species, the fits of both homo- and heteroscedastic models were equal (model pair 5, Table 1). TI host species had, on average, lower asymmetry than TP species, but this difference was not significant (TI: −0·15, TP: 0·04; $t_{88} = −1·05$, $P = 0·29$). Similarly, within the parasite community, both homo- and heteroscedastic models equally fitted (model pair 6, Table 1). In contrast to hosts, TI parasites had a significantly lower Ai than TP parasites (TI: −0·61, TP: −0·37; $t_{248} = 3·1$, $P = 0·002$).

Within the host community, the temporal variation in centrality was unequal between TI and TP species (model pair 7, Table 1). The model showed that across years, the

species-average BC of TP hosts was significantly higher than that of TI species (0·24 vs. 0·003, respectively; $t_{88} = -7.0$, $P < 0.0001$). In addition, the coefficient estimate for temporal variation in the BC of TI hosts was 0·003 times that of TP hosts, indicating that TI species were invariably peripheral across years because a low variance coefficient indicated a lack of temporal variation.

Within the parasite community, variation in centrality was unequal between TI and TP species (model pair 8, Table 1). The centrality of TP parasites was significantly higher than that of TI parasites (0·21 vs. 0·03, respectively; $t_{248} = -7.9$, $P < 0.0001$). The coefficient estimate for the temporal variation in the centrality of TI parasites was 0·29 times that of TP hosts. Although not to the same extent as in hosts, this indicated that TI parasites retain their peripheral role across years.
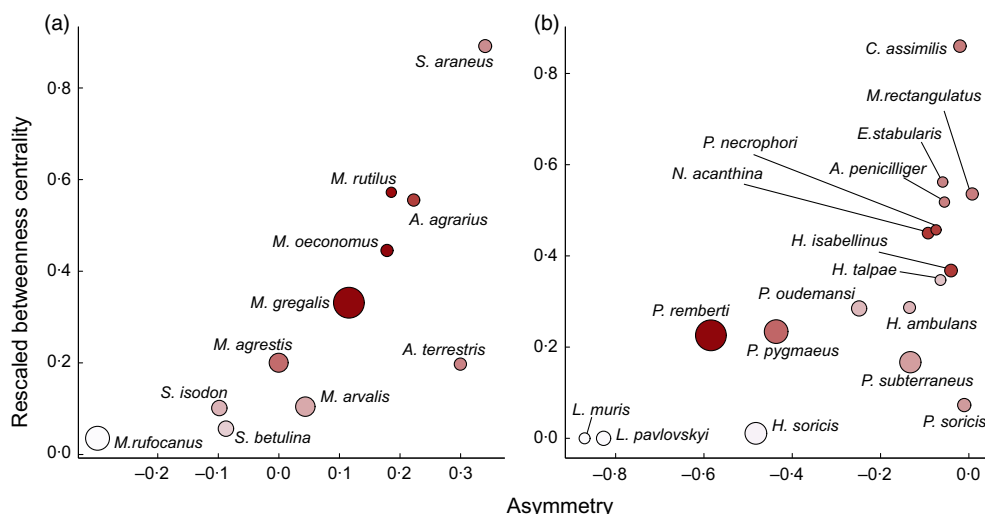
RELATIONSHIP BETWEEN ASYMMETRY AND CENTRALITY

There was a significant positive linear correlation between Ai and BC for core hosts and parasites ($r = 0.76$ and $r = 0.69$, respectively; $P < 0.01$ for both) (Fig. 2). It can also be seen in Fig. 2 that, in general, hosts that exerted more direct influence (higher values of Ai) had lower temporal variation in Ai, but not necessarily low temporal variation in BC. Similarly, parasite species that were less prone to direct influence by hosts (Ai close to 0) had lower temporal variation in Ai, but medium-to-high temporal variation in BC.

Discussion

Earlier studies have focused on the temporal dynamics of species/interaction turnover in mutualistic (Petanidou

et al. 2008; Alarcón, Waser & Ollerton 2008; Dupont et al. 2009; Olesen, Stefanescu & Traveset 2011) or antagonistic (Laliberté & Tylianakis 2010) networks and in food webs (Schoenly & Cohen 1991). In this study, we take a step further and examine, for the first time, the temporal dynamics of functional roles of species in an antagonistic network by directly examining the temporal variation component. It should be noted, though, that our analysis has three main limitations. First, the negative relationship between parasite abundance and host fitness may not be linear, so that a parasite with a low value of asymmetry could have a major effect on its host. For example, parasitism may cause energy loss in a host due to mounting of an immune response (Lochmiller & Deerenberg 2000). Yet, due to the complexity and multiple interactions involved in asymmetry, we cannot predict the exact effects of a nonlinear relationship on values of asymmetry or BC. Second, the effect of parasites on host fitness was quantified for a few host–parasite associations only (e.g. Arnold & Anja 1993; Neuhaus 2003), while for the majority of parasites the magnitude of the effect is unknown. We thus assumed that parasites were similar in their negative effects on hosts. Third, we used host species for which at least 10 individuals were captured. This threshold increased the robustness of the analysis but we may have omitted some rare host species. However, rare species are usually intermittent, and thus, we believe that the omission of few rare species would not have qualitatively affected the results. Nonetheless, as we discuss below, if the effects of intermittent species are nonlinear, then rare species may have a disproportional influence, which we may have missed. Despite these limitations, this study provides first and valuable insights into the temporal dynamics of the functional roles hosts and parasites play in the system, which has not been studied

Fig. 2. Correlation between asymmetry and rescaled betweenness centrality (BC) for (a) 11 host and (b) 17 parasite species that occurred in the network for 6 years. The size of the circle represents relative temporal variation in asymmetry (larger circle corresponds to greater temporal variation in asymmetry). Circle shade (colour in the online version) represents relative temporal variation in BC (darker shade corresponds to greater temporal variation). Values for circle size and shade are relative to the bar heights in Fig. 1.

so far. Below, we discuss our results according to the hypotheses we posed and then discuss further consequences of our findings.

TEMPORAL DYNAMICS OF CORE SPECIES

The network dynamics resulted in strong among-species heterogeneity in the temporal variation in asymmetry and centrality. Therefore, our hypothesis that temporal variability in direct and indirect influences would differ across species within a community (H1) is not rejected. However, it requires explaining why temporal variation in asymmetry and/or centrality is high in some of the core species, but low in others.

Temporal variation in asymmetry is affected by both evolutionary and ecological processes (Carnicer, Jordano & Melián 2009). Heterogeneity in asymmetry may stem from among-species differences in some traits. For instance, some host species may be characterized by large yearly fluctuations in abundance, resulting in fluctuations in the resources provided to parasites exploiting them, here observed as high temporal variation in asymmetry, while the abundance of other host species remains temporally stable (Bjornstad, Falck & Stenseth 1995). Within host species, traits that affect parasite abundance (e.g. immunocompetence, body mass) or a parasite species' ability to infest a host (e.g. host detection ability) are not expected to vary greatly across years (Arneberg, Skorping & Read 1997; Krasnov *et al.* 2006), and thus, intraspecific temporal variation in asymmetry is not expected to be high. This is supported by generally low within-species temporal variation in asymmetry, with only a few species having high temporal variation. Environmental stochasticity may explain at least part of the high interspecific temporal variation. For example, unusually cold weather can delay the development of only a subset of ectoparasite species that are highly sensitive to climatic fluctuations (Krasnov *et al.* 2001). Climatic fluctuations have also been suggested to affect temporal variation in the structure of a mutualistic network (Alarcón, Waser & Ollerton 2008). Parasite abundance has been shown to be a true species-related trait in the sense that it varies within host species in rather narrow boundaries (Krasnov *et al.* 2006). Because here asymmetry is based on mean parasite abundance values, we suggest that highly influential host species may be those which are consistently more parasitized than others.

In contrast to asymmetry, centrality is strongly affected by the availability of other species in the system, and thus, the yearly species/interaction turnover resulted in high temporal variation in centrality both within and across species. Some host–parasite associations are characterized by cyclic fluctuations in the abundances of the host and, with a certain lag, parasite species (Hudson, Dobson & Newborn 1998). Based on our results, we suggest that temporal variability in species centrality may be correlated with cyclic changes in abundance. When host abundance is at its peak, host individuals are more likely to be parasitized, in addition to their typical parasites, by parasite species that are less specific to the host because the probability of host-to-host transfer increases with host abundance (Krasnov, Khokhlova & Shenbrot 2002). This will increase the probability that the host species will share parasites with other hosts, translated to high centrality of the host species. When host abundance is low, it will be parasitized mainly by a group of parasites more specific to it, lowering the probability of sharing parasites with other host species, making it less central. From a parasite species' perspective, an increase in its preferred host abundance will increase its own abundance (Arneberg *et al.* 1998), thus making it more central as it will also infest host species other than its preferred one. When the abundance of the parasite is low, it will be less central as it will be mostly restrained to its preferred host. This process may occur in our system as fleas are opportunistic parasites, which are usually specific to a main host but can also switch to a less preferred one (Krasnov 2008).

DYNAMICS OF TEMPORALLY PERSISTENT AND INTERMITTENT SPECIES

Temporally persistent hosts promoted parasite transmission across the network and TP parasites facilitated parasite transmission, but the extent of their influence varied among years. In contrast, TI hosts and parasites were invariably peripheral across years. Therefore, we do not reject our hypothesis H2 and our results suggest that TP hosts are the ones that drive the system as none of the TP parasites were influential. However, these seemingly 'weak effects' of TI species should not be underestimated (Berlow 1999). TI hosts may act as latent reservoirs of opportunistic but strongly influencing parasites that may be transferred to other hosts via a central TP host in a certain year – a transmission pattern similar to disease outbreaks (Paull *et al.* 2012).

ACROSS-SPECIES CORRELATION BETWEEN DIRECT AND INDIRECT INFLUENCE

The positive correlation between asymmetry and centrality indicates that hosts that exert strong positive influence on parasites (relative to the weak negative effect parasites exert on them) also exert strong indirect influence on other hosts, probably by facilitating parasite transmission. Similarly, parasites that exert strong negative direct influence on hosts (relative to the weak positive effect hosts exert on them) also exert strong indirect influence on other parasites, probably by facilitating host exploitation by multiple parasites (Krasnov *et al.* 2005). These patterns support our initial hypotheses.

Despite a positive correlation between asymmetry and centrality, there was much variation in centrality in parasites with asymmetry values close to zero. Therefore, the direct effect of a parasite on its host is not necessarily

related to its functional role in facilitating infestation of hosts by other parasites. Five hosts (*A. agrarius*, *M. rutilus*, *M. oeconomus*, *S. araneus* and, to a lesser extent, *Arvicola terrestris*) were, on average, more exploited by ectoparasites (high asymmetry) and propagated transmission (high centrality), whereas others played a less important role. Vázquez *et al.* (2007) found a significant correlation between species abundance and asymmetry, whereby more influential species should be the most abundant ones. This hypothesis should be examined using estimates of abundance independent of those used for network construction, but a preliminary analysis based on our abundance data only partially supported it (Fig. S7, Supporting information). Therefore, observed patterns in interaction asymmetry cannot be explained by host abundance alone, as also noted by Vázquez *et al.* (2007).

CONSEQUENCES OF TEMPORAL DYNAMICS

Taken together, our results point to a core of TP hosts and parasites that drive the system, in terms of parasite propagation and infestation facilitation, with TI peripheral species playing a minor role. However, even within the group of core species, some species exhibit large temporal variation, such that the functional roles they play change over time despite their temporal persistence. Temporal variation in a functional role is a consequence of changes in interactions, which can be caused by either species turnover or rewiring (change in interactions among occurring species). Among the core species, variation in a functional role is the result of rewiring because there is no species turnover. The ability to rewire interactions increases overall network stability (Ramos-Jiliberto *et al.* 2012). Furthermore, it ensures that parasites will always be transmitted across hosts because, when a host is less central in a certain year, there is a substantial likelihood that another host will take its place. This results in a resilient network which is also temporally stable in its global properties, as suggested by the observed network connectance and as has been shown in mutualistic networks (Petanidou *et al.* 2008; Olesen, Stefanescu & Traveset 2011).

Finally, understanding the dynamics of species' functional roles is important from a disease ecology perspective. In our model of small mammals and fleas, the temporal variation we find can have consequences for the transmission dynamics of vector-borne pathogens and eventually for the risk of zoonotic vector-borne diseases, such as plague (Girard *et al.* 2004). Further exploring the temporal variation in species roles in antagonistic networks using additional species roles will provide important insights that may be later applied for selection of the most appropriate target hosts for control.

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Data accessibility

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Yearly species accumulation curves.

Appendix S2. R code for analyses.

Fig. S1. Histograms showing (a) number of species (hosts – blue; parasites – orange) in the network for a certain number of years (persistence) and (b) frequency of links in the network for a certain number of years.

Fig. S2. Yearly (1982–1987) bipartite host–parasite interaction networks. For each network, parasite and host species are represented as boxes at the top and at the bottom, respectively, and the thickness of the links is proportional to the mean number of parasites found on individual hosts. Numbers are species IDs from Table S1.

Fig. S3. Asymmetry index (Ai) calculated directly from the network data for the 11 host species that occurred in the network for 6 years. Dashed blue line is fixed at zero and represents a lack of asymmetry in direct influence.

Fig. S4. Asymmetry index (Ai) calculated directly from the network data for the 17 parasite species that occurred in the network for 6 years. Dashed blue line is fixed at zero and represents a lack of asymmetry in direct influence.

Fig. S5. Values of rescaled betweenness centrality calculated directly from the network data for 11 host species that occurred in the network for 6 years.

Fig. S6. Values of rescaled betweenness centrality calculated directly from the network data for 17 parasite species that occurred in the network for 6 years.

Fig. S7. Within-year Spearman correlation between total abundance (total number of individuals collected per species) and asymmetry index of host species. Significance values are written within each panel.

Table S1. Summary of species occurrence in the yearly networks.