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Latitudinal mismatches between the components of mammal–flea interaction networks

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ABSTRACT

Aim The large-scale description of ecosystem complexity, including the structure of interaction networks, has been largely overlooked although it is known to underpin species co-occurrences and their robustness to climatic or anthropogenic disturbances. Here, we investigated whether the various components of mammal–flea interaction networks (richness of fleas, richness of mammals and the richness of mammal–flea associations) are spatially congruent and follow the latitudinal diversity gradient (LDG).

Location Sixteen regions, world-wide.

Methods We first took into account the effect of area on diversity by determining the position of regions with respect to species–area relationships. We then investigated the spatial congruence between the regional richness of each component of mammal–flea interaction networks as well as their latitudinal gradients. We further investigated patterns for flea–host associations by testing for relationships between mammal–flea interaction richness and (1) flea niche breadth and (2) host carrying capacity.

Results We report divergent LDGs for the different components of mammal–flea interaction networks: our data agree with a canonical LDG for mammals, but reveal that the diversity of fleas and mammal–flea associations do not follow such a classical gradient. Our results suggest that host carrying capacity is more likely than flea niche breadth to modulate the number of links in host–parasite interaction networks.

Main conclusions The complex interplay between geographic variation in host diversity and both host and parasite traits can lead to unexpected spatial patterns such as the invalidation of expected parasites and links in host–parasite web LDGs. Beyond our focus on host–parasite interactions, our study is among the first in the emerging field of interaction network macroecology and paves the way for other components of ecological networks to be investigated across space and time.

Keywords

Carrying capacity, fleas, host–parasite, interaction network, latitudinal gradient, mammals, niche breadth.

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INTRODUCTION

One of the most striking features of biodiversity is its spatial heterogeneity (Gaston, 2000). However, a restricted set of general rules seems to govern this heterogeneity over macroecological scales. In particular, species richness increases with the

size of the sampling area (the species–area relationship, SAR; Rosenzweig, 1995) and when moving from temperate toward tropical regions (the latitudinal diversity gradient, LDG; Gaston, 2000; Hillebrand, 2004). Although the magnitude of increase in species richness with decreasing latitude and increasing area may vary with respect to biological traits or ecological

conditions (Currie, 1991; Hillebrand, 2004; Drakare *et al.*, 2006; Guilhaumon *et al.*, 2008), these two patterns are remarkably consistent across plant and animal taxa (micro- to macro-organisms), environments (terrestrial versus aquatic) and time (Rosenzweig, 1995; Willig *et al.*, 2003). Global-scale SARs are linked to the LDG because tropical regions accumulate more species than would be expected from their area compared with temperate and polar regions (Hillebrand, 2004; Lamoreux *et al.*, 2006).

With the mounting recognition of the multi-faceted nature of biodiversity, recent investigations generally tend to confirm and provide explanations for the LDG. For example, opposing latitudinal gradients are found in the diversification and extinction rates of organisms on a global scale, creating a phylogenetic diversity gradient which in turn should contribute to the general latitudinal trend in species richness (Jablonski *et al.*, 2006; Wiens, 2007).

Another facet of biodiversity, the structure of networks of ecological interactions, has long been recognized as central to ecology (Darwin, 1859) but has only recently been incorporated into the description of ecosystem complexity (Bascompte, 2009). Studying the structure of ecological networks would provide new insights into the assessment of network robustness to perturbations such as climate change or anthropogenic disturbances (Díaz *et al.*, 2006; Bascompte, 2009; Tylianakis *et al.*, 2010; Araújo *et al.*, 2011) and extinction dynamics (Petchey *et al.*, 2008). However, macroecological trends in the structural attributes of interaction networks, such as the diversity of links, are still virtually unknown (but see Schemske *et al.*, 2009, for a recent review).

Host–parasite webs are both a representative and challenging model for investigating large-scale patterns in the structure of interaction networks. This is because parasites, through their interactions, can deeply modify the structure of food webs and thus affect energy flows within ecosystems and the dynamics of infectious diseases (Lafferty *et al.*, 2008). At first glance, because parasites and hosts are involved in intimate interactions, one might hypothesize that large-scale patterns in parasite richness should mirror those of their hosts (Poulin & Rohde, 1997). Hence, despite equivocal empirical evidence and in part because information on large-scale patterns in the distribution of invertebrate species is limited, spatial congruence between macroecological patterns for parasites and their hosts is generally assumed (e.g. Harris & Dunn, 2010). However, depending on parasite characteristics such as phylogeny, feeding type or transmission mode, only weak and inconsistent evidence has accumulated in favour of parasite LDGs (Poulin & Morand, 2004; Lindenfors *et al.*, 2007; Bordes *et al.*, 2010; but see Dunn *et al.*, 2010, for human pathogen richness). The prevalence of such counter-intuitive results is still poorly understood (e.g. Poulin, 2001; Lindenfors *et al.*, 2007; Bordes *et al.*, 2010).

At large scales, host–parasite associations are under phylogenetic constraints and vary with latitude following the latitudinal niche breadth hypothesis (Vázquez & Stevens, 2004; Krasnov *et al.*, 2008). This hypothesis, proposed in the middle of the 20th century (Dobzhanski, 1950), posits that the latitudinal gradient

in environmental conditions (from stable and benign in the tropics to markedly seasonal and severe at high latitudes) has led to the evolution of a higher proportion of specialist species in the tropics than at higher latitudes. Accordingly, in addition to the number of host and parasite species present in a region, parasite specificity, which is negatively related to parasite niche breadth, or alternatively to the carrying capacity of hosts in terms of the diversity of parasite species they can harbour, are likely to shape the number of links realized in host–parasite webs. Hence, the existence of latitudinal gradients in the diversity of links in host–parasite networks is far from trivial since it is potentially influenced in opposite directions by different forces. Among hosts, diversity should increase towards the tropics, but carrying capacity should decrease (Bordes *et al.*, 2010). It is expected that parasites should show the same LDG as their hosts, but parasite niche breadth should increase polewards (Krasnov *et al.*, 2008). Testing for spatial congruence between the geographic distribution of parasite and host diversity will allow a deeper knowledge of their relationship (Krasnov *et al.*, 2004b, 2007). In addition to the theoretical importance of studying gradients, from a practical point of view the recognition and identification of large-scale gradients in link diversity for host–parasite webs is crucial for public health and environmental risk management (Dunn *et al.*, 2010).

Here our objective is to investigate the LDG for different components of regional host–parasite networks: number of mammal species, number of infected mammal species, number of flea species and the number of links, i.e. the number of mammal–flea associations that is a measure of interaction diversity (Tylianakis *et al.*, 2010). We tested the congruence of these four host–parasite network components using data from 16 regions around the world at different latitudes. Our results suggest that parasite diversity depends more on the ecological and evolutionary characteristics they share with the hosts they infect than on the diversity of their potential hosts (Poulin & Morand, 2004; Dobson *et al.*, 2008). Consequently, we found no latitudinal gradient in the richness of fleas and the diversity of links in mammal–flea webs, despite the latitudinal gradient in mammal richness.

METHODS

Flea and mammal data

Data on fleas and mammals were obtained from published regional monographs encompassing 16 regions on six continents (Appendix S1 in Supporting Information). These sources are based on comprehensive information taken from numerous publications, museum records and unpublished information, and they provide the best available information for global studies at the level of entire faunas, including interaction richness. We based our analyses on region-wide numbers of: (1) flea species, (2) mammal species that were found to be infected by fleas, (3) all mammal species (excluding cetaceans and pinnipeds), and (4) realized links (observed number of host–parasite associations). Among the variety of available monographs on

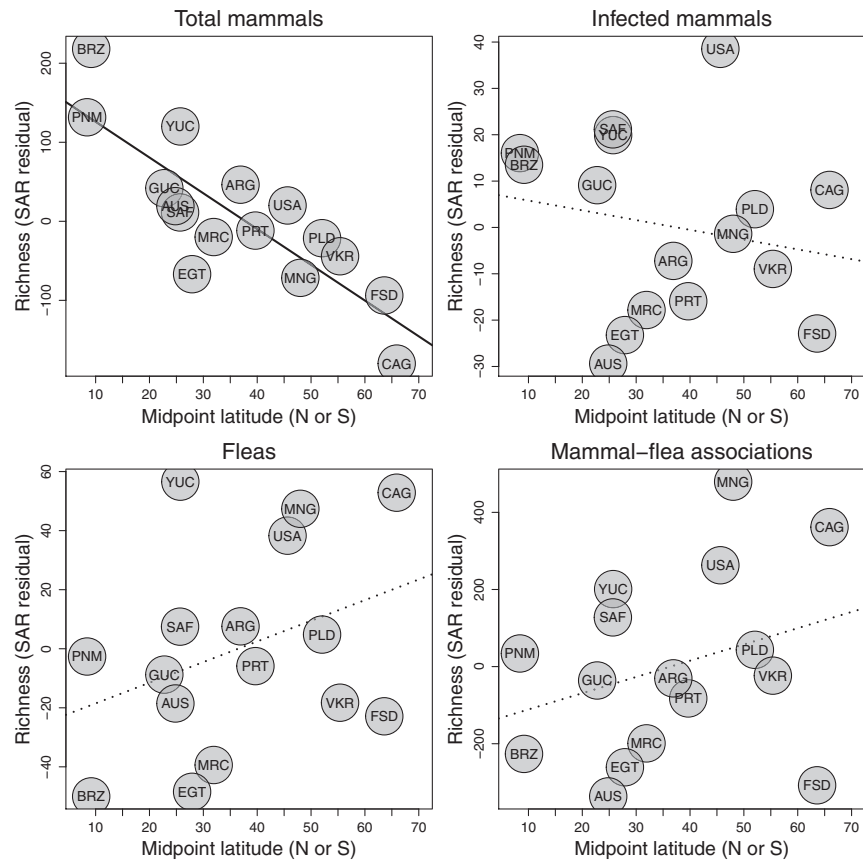


Figure 1 The relationship between latitude (absolute north or south latitudinal midpoint) and the richness of the different components of the mammal–flea interaction networks (indicated as residuals from the species–area relationship, SAR). Plain and dotted lines are respectively significant and non-significant linear regressions at the 5% level. Abbreviations of region names are: ARG, Argentina; AUS, Australia; BRZ, Brazil; CAG, Canada, Alaska and Greenland; EGT, Egypt; FSD, Fennoscandia and Denmark; GUC, Guizhou province of China; MNG, Mongolia; MRC, Morocco; USA, Pacific Northwest of the USA; PNM, Panama; PLD, Poland; PRT, Portugal; SAF, South Africa; VKR, Volga–Kama region of central Russia; YUC, Yunnan province of China.

flea faunas, we used only those that presented information on records of each particular flea species on each particular mammal species. We cross-checked the species lists with the catalogues of Lewis & Lewis (1990) for fleas and Wilson & Reeder (2005) for mammals to resolve cases of synonymy. Region area was estimated from maps or descriptions provided in original sources. The 16 regions used in this study (Fig. 1, Appendix S1): (1) total 43,185,248 km² (c. 30% of the earth's total land mass), (2) vary greatly with respect to area, (3) are spread over six continents, and (4) encompass a wide range of latitudes, longitudes and climatic conditions.

Statistical analyses

To investigate LDGs for the different components of mammal–flea interaction networks we first had to account for the effect of area on diversity (i.e. the SAR). Indeed, inference about the SAR is mandatory in the wide range of macroecological applications that require the comparison of diversity patterns when regions differ in area (Smith, 2010). Various shapes of SAR have been described in the literature (Tjørve, 2009) and no real consensus has emerged regarding a 'ubiquitous' model across all taxa and environmental conditions (Connor & McCoy, 1979; Stiles & Scheiner, 2007; Guilhaumon *et al.*, 2008). SARs are influenced by environmental conditions, species traits and demographic processes, and these processes diverge in some aspects between parasites and their hosts. Thus, accounting for potential differ-

ences in the shape of SARs in comparative analyses may improve our ability to distinguish whether a force that drives the macroecological pattern of one biodiversity component also drives the pattern of another component in the same direction. Here, in order to cope with uncertainties in SAR modelling and potential differences between SARs for the different components of mammal–flea interaction networks, we removed the effect of area on the number of flea species, infected host species, all host species and flea–host associations using the multi-model SAR approach proposed by Guilhaumon *et al.* (2008). Briefly, this approach handles differences and uncertainties in SARs by fitting a collection of SAR models and then averaging between all models whilst weighting according to the relative support given to them by the data (Appendix S2).

To determine whether the richnesses of the different components of mammal–flea interaction networks are spatially related, we examined the Pearson's correlation coefficient between the residuals from multi-model SARs. We also used ordinary least squares (OLS) regression analyses to investigate the relationships between the regional richness of each component of mammal–flea interaction networks and latitude (the mid-point latitude for each region was calculated at the centroid of each region's polygon).

In order to further investigate the patterns related to the geographic variation in the diversity of flea–host associations, we used OLS regression analysis to test for relationships between mammal–flea interaction richness (after accounting for the

SAR) and: (1) the average number of hosts per flea species (which we considered as a proxy for flea niche breadth), and (2) the average number of fleas per host species (which we considered as a proxy for host carrying capacity).

As in most macroecological studies, spatial autocorrelation may have biased parameter estimates of the regression models (Dormann *et al.*, 2007) and thus led to spurious conclusions about the ranking of regions with respect to multi-model SARs (Giam *et al.*, 2011). We tested for spatial autocorrelation in the residuals of multi-model SARs using Mantel permutation tests (Legendre & Legendre, 1998). Mantel tests were conducted between the matrix of pairwise great circle distances between regions (based on the coordinates of the centroid of each region) and the pairwise matrices of Euclidean distances between regions calculated from multi-model SAR residuals. None of the components of mammal–flea interaction networks exhibited spatially autocorrelated multi-model SAR residuals, justifying the use of OLS regressions (Appendix S2). Additionally, we checked the robustness of our results to the use of the sequential strategy we devised to analyse the dataset (investigating the latitudinal trends of regional diversity as determined by the residuals of multi-model SARs). To check robustness, we built multiple regression models to evaluate both the significance and the independent contributions of area and latitude to the total variation in the four richness response variables (number of mammal species, number of infected mammal species, number of flea species and number of flea–host associations). The two approaches led to equivalent conclusions (Appendix S2).

All analyses described above were implemented within the R statistical programming environment, with SAR analyses performed using the R package ‘mmsar’ (Guilhaumon *et al.*, 2010; <http://mmsar.r-forge.r-project.org>). Spatial manipulations were achieved using the Quantum GIS 1.6.0 software (<http://www.qgis.org>).

RESULTS

All tested SAR models fit all datasets, with the exception that the exponential model did not fit the SAR of infected mammals (Appendix S2). Comparison of model selection patterns revealed general uncertainty about SAR shape with no one model consistently outperforming the others [all Akaike second-order information criterion (AICc) weights < 0.80 in Appendix S2]. These uncertainties and multiple adequate fits together justify the use of multi-model SARs when taking into account the effect of area on diversity in the present study (see Appendix S2 for further details about SAR analyses).

Correlations between pairs of network components across regions, after controlling for area, were highly variable (Table 1). A strong positive and significant correlation was found between the number of flea–host associations and flea species richness. Correlations between flea species richness and the number of infected hosts as well as between the number of infected hosts and the number of mammal–flea associations in each region were also significant, albeit weaker (Table 1). There was no significant correlation between total mammal species richness and

Table 1 Pearson’s correlations among regional richness values of the different components of mammal–flea interaction networks.

	Total	Infected	Fleas	Links
Total	–	0.122	0.452	0.441
Infected	0.402	–	0.027	0.007
Fleas	–0.203	0.551	–	0.000
Links	–0.207	0.644	0.895	–

Pearson’s correlations are presented in the lower part of the table and associated *P*-values in the upper part. Total = total mammal richness; Infected = infected mammal richness; Fleas = flea richness; Links = mammal–flea link richness.

either the number of mammals infected with fleas, flea species richness or the number of mammal–flea associations (Table 1).

We found a strong and significant latitudinal gradient in mammal species richness (Fig. 1). This trend corresponds to a decrease of 4.52 mammal species per degree of latitude. For all three other components of mammal–flea interaction networks, no latitudinal trend was detected (all regressions were non-significant; Fig. 1).

Host carrying capacity was significantly and positively correlated with the richness of mammal–flea interactions. In contrast, flea niche breath was only marginally and negatively correlated with the richness of mammal–flea interactions (Fig. 2).

DISCUSSION

The LDG is among the most general and best documented ecological patterns (Gaston, 2000), and although the role of biotic interactions is a pervasive theme in efforts to understand these patterns (Schemske *et al.*, 2009), global-scale comprehensive analyses of the biogeography of parasites and pathogens have only recently begun to be undertaken (Guernier *et al.*, 2004; Lindenfors *et al.*, 2007; Smith *et al.*, 2007; Dunn *et al.*, 2010). Our study assesses the global concordance between the diversity of different components of regional mammal–flea interaction networks and provides insights into disentangling the inconsistent patterns detected in recent studies of the macroecology of parasites and pathogens (Lindenfors *et al.*, 2007; Dobson *et al.*, 2008; Dunn *et al.*, 2010).

Assessments of LDGs generally report an increasing polar-to-equatorial trend whatever the biodiversity component measured (Gaston, 2000; Hillebrand, 2004). Surprisingly, our analysis of regional mammal–flea interaction networks shows that for parasites, for the fraction of potential hosts infected by parasites and for the diversity of host–parasite interactions, this pattern is not observed. Although based on the analysis of a limited number of regions, these results are compatible with previous findings for global-scale mammal studies (e.g. Ceballos & Ehrlich, 2006). For fleas (and more generally for ectoparasites), to our knowledge, no global-scale study exists but, for example, the flea fauna of the Palaearctic is known to be richer than in any other biological realm. This is the outcome of evolutionary processes and patterns of dispersal over time, and not merely of

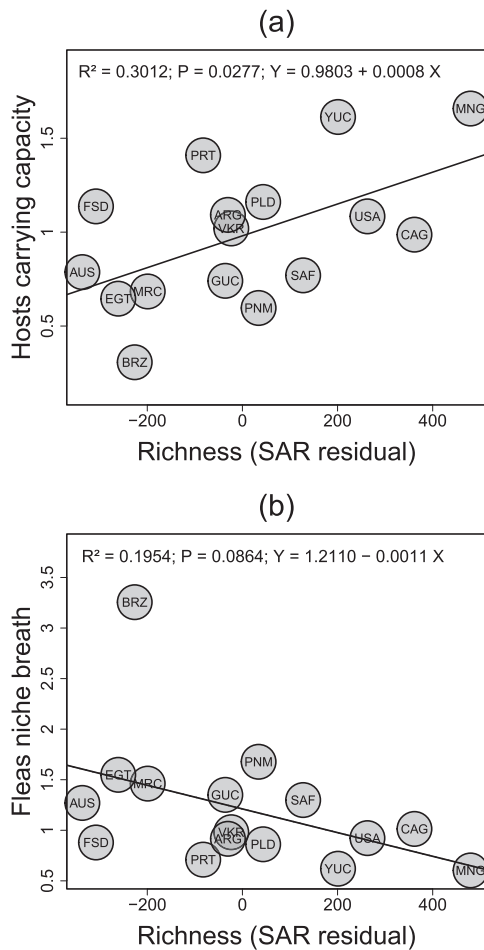


Figure 2 The relationship between mammal–flea interactions richness (links richness) and: (a) host species carrying capacity and (b) flea species niche breadth. Abbreviations of region names are: ARG, Argentina; AUS, Australia; BRZ, Brazil; CAG, Canada, Alaska and Greenland; EGT, Egypt; FSD, Fennoscandia and Denmark; GUC, Guizhou province of China; MNG, Mongolia; MRC, Morocco; USA, Pacific Northwest of the USA; PNM, Panama; PLD, Poland; PRT, Portugal; SAF, South Africa; VKR, Volga–Kama region of central Russia; YUC, Yunnan province of China.

variation in study effort (see Medvedev, 1996, 2000a,b, 2005; Krasnov, 2008). We observed that the correlations between the total number of mammal species and the richness of all the other components of mammal–flea interaction networks were not significant, whereas the number of fleas correlated strongly and significantly with the number of infected mammals and the number of flea–host associations (Table 1). These results suggest that at a regional scale, top-down processes involving the complex interplay between the responses of parasites to their host's ecology and evolutionary history and direct environmental constraints can drive the diversity of host–parasite interactions. This ultimately generates patterns at odds with classic macroecological predictions.

Previous studies have highlighted the concordance between the macroecological responses of hosts and their parasites. For example, Rapoport's effects have been detected for both the spatial (geographic range size) and biological (host specificity) components of niche breadth in fleas (Krasnov *et al.*, 2008). These results are compatible with our findings of strong correlations between patterns for infected mammals and fleas richness (Table 1). Whilst previous studies have compared the richness of parasites with the richness of their hosts and not with the richness of the overall fauna of potential hosts, we show that analysing the richness of both infected and all mammals in a region may help to disentangle the contradictory LDGs reported previously (e.g. Lindenfors *et al.*, 2007).

Even though parasites share many biogeographic characteristics with their hosts (Lindenfors *et al.*, 2007; Krasnov *et al.*, 2008), this does not imply that all the structural properties of host–parasite networks follow the same trend over macroecological scales. Host–parasite relationships are strongly phylogenetically constrained (Poulin & Rohde, 1997; Krasnov *et al.*, 2004a; Mouillot *et al.*, 2008) and we may therefore expect an impact of evolutionary forces on large-scale patterns of host–parasite networks. More precisely, flea niche breadth (negatively related to specificity for their hosts; Krasnov *et al.*, 2008), and host carrying capacity (the number of flea species a host can harbour) could determine the number of realized links in host–parasite webs and *in fine* modulate the apparent influence of host species richness. Our analysis and previous ones (Lindenfors *et al.*, 2007; Krasnov *et al.*, 2008) suggest that both hypotheses are plausible, although the latter seems to be better supported by our data set (Fig. 2). Indeed, if the diversity of mammal–flea interactions was predominantly related to the geographic variation in the niche breadth of fleas, then fleas with broad niches in a region could produce a high number of mammal–flea interactions independently of the number of flea species. Thus, the strong correlation that we observed between flea species richness and the diversity of mammal–flea interactions (Table 1) would not be expected.

Overall, the results of our analyses underline that hosts and parasites have neither the same ecological opportunities nor the same constraints. Fleas, although undoubtedly subject to the biogeography of their hosts, also experience their own ecological and evolutionary constraints. The complex interactions between these forces can invalidate the classical expectation that large-scale patterns in parasite richness mirror those of their hosts. Beyond our focus on host–parasite interactions, our study is among the first in the emerging field of the interaction network macroecology to study macroecological interactions using network analyses. Our results pave the ways for other components of ecological networks, such as nestedness and modularity, to be investigated across space and time. The description and the comprehension of such patterns may, among other things, help elucidate invasion processes (Sugiura, 2010), food-web persistence (Stouffer & Bascompte, 2011) and the response of assemblages to climate change (Araújo *et al.*, 2011).

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SUPPORTING INFORMATION

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

Appendix S1 Summary of data on fleas, their mammalian hosts and areas of different regions.

Appendix S2 Supplementary methods and results: species–area relationship (SAR) analyses, assessment of methods robustness and spatial autocorrelation.

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BIOSKETCH

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