Parasitol Res (2012) 111:393–401
DOI 10.1007/s00436-012-2850-9

ORIGINAL PAPER

Evolutionary co-variation of host and parasite diversity—the first test of Eichler's rule using parasitic lice (Insecta: Phthiraptera)

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Received: 14 January 2012 / Accepted: 1 February 2012 / Published online: 15 February 2012

Abstract The taxonomic richness of lice (Phthiraptera) varies considerably among their avian and mammalian hosts. Previous studies explored some factors shaping louse diversity; however, the so-called Eichler's rule—according to which taxonomic richness of parasites co-varies with that of their hosts—has never been tested. Our study incorporates all families of birds and mammals and the whole order of lice to test this co-variation, thus we present the widest taxonomic range to test any correlates of louse richness. Louse richness data were controlled for uneven sampling effort. We used the method of independent contrasts to control for phylogenetic effects. We found a strong correlation between the species richness of avian and mammalian families and generic richness of their lice. We discuss some alternative macroevolutionary and macroecological hypotheses that may explain this phenomenon that may well be a general feature of parasitism and it seems possible that this effect contribute considerably to global biodiversity.

Introduction

Parasitism is a successful way of life, as—depending on the definition of parasitism—6–50% of known animal species are parasites (Poulin and Morand 2004). They influence almost every aspect of the life history of non-parasitic species (Thomas et al. 2005). Hence, arriving at an understanding of the factors shaping parasite biodiversity on a global scale is a major task for macroecological and macroevolutionary research. Given that parasites tend to be highly specific to their host resources, it seems reasonable to expect a positive co-variation between the taxonomic richness of hosts and that of their parasites. Eichler (1942) was the first to point out this relationship and it was dubbed as 'Eichler's rule' (Stammer 1957) later on. Admittedly, this co-variation might seem obvious. However, even theoretically expected relationships need to be verified by using a wide range of empirical data and modern methodologies for at least two reasons. Firstly, we expect such tests to yield new information about the strength of the relationship. Secondly, we also hope to obtain information about potential differences among different taxa in the strength of this relationship. Take "Fahrenholz's rule" (Fahrenholz 1913) as an example. It seemed to be a triviality to presume a topological similarity of host and parasite phylogenetic trees. However, as rigorous tests have later provided contradictory results among different taxa, testing this 'trivial rule' has established a new discipline within evolutionary biology (Page 2003).

Here we set out to test this presumed relationship by using data on the order of lice (Insecta: Phthiraptera). Lice traditionally played an important role in the study of host–parasite evolution (Johnson and Clayton 2003; Page 2003) for two major reasons. Firstly, extensive sampling effort through several centuries resulted in a considerable amount of data concerning their taxonomical richness, distribution,

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and host specificity (Price et al. 2003). Secondly, lice are very intimately related to the host individual spending their entire life-cycle in the host pelage or plumage. Several authors showed that lice affect both the life expectancy (Barbosa et al. 2002; Booth et al. 1993; Brown et al. 1995; Papp et al. 2005) and reproductive success (Clayton 1990; Kose and Møller 1999; Kose et al. 1999) of their hosts. Additionally, lice also act as vectors of virulent microbial infections (see e.g. Clayton et al. 2008; Raoult and Roux 1999). Lice are classified into four suborders: Amblycera, Ischnocera, Rhynchophthirina, and Anoplura (Price et al. 2003). However, recent studies (Johnson et al. 2004; Murrell and Barker 2005; Smith et al. 2011) suggested that Phthiraptera do not form a monophyletic group. The parasitic way of life appeared two times independently in parasitic lice: once in the ancestors of Amblycera and once in the ancestors of the other three suborders. Diversity and hosts of louse taxa is summarized in Table 1 following Johnson and Clayton (2003). Lice were generally considered quite host specific (Mey 2003), however, it seems that their host specificity varies on a large scale (see e.g. Hellenthal and Price 1991; Price 1975; Price et al. 2003, Zuo et al. 2011).

It is reasonable to separate louse suborders (and even families of avian lice) in comparative analyses because their life histories and the factors shaping their distribution and evolution are quite different, as already shown by several former studies (see e.g. Hughes and Page 2007; Møller and Rózsa 2005; Møller et al. 2010; Price et al. 2003; Vas et al. 2011; Whiteman et al. 2006).

Since Felsenstein (1985), it had been widely accepted that comparative studies have to take evolutionary history into account, as traits of related taxa are statistically non-independent. Moreover, comparative studies focused on parasite richness among host taxa can also be confounded by uneven sampling effort of parasites (Krasnov et al. 2005; Poulin 2007; Walther et al. 1995), hence researchers need to control both for phylogenetic effects and uneven sampling effort while studying macroevolutionary patterns of parasite richness and distribution. Additionally, the uncertainty of louse morphospecies concept and an overestimation of parasite species richness of widely distributed hosts also act as a potential bias in the quantification of louse taxonomic richness (see below).

Previous authors have already explored some factors correlated with the taxonomic richness of lice. Past bottleneck effects of host populations (MacLeod et al. 2010; Paterson et al. 1999; Rózsa 1993) and host aquatic lifestyle (diving under the water surface for food) (Felső and Rózsa 2006, 2007) reduce louse richness. Preening and other behavioral defenses against ectoparasites were also suggested to reduce louse richness, however, the evidence is limited (Clayton and Walther 2001; Clayton et al. 2010). Host innovative capabilities (Vas et al. 2011) and defenses such as stronger immune responses (Møller and Rózsa 2005) or relatively larger uropygial glands (Møller et al. 2010) co-vary positively with Amblyceran taxonomic richness but not with Ischnocerans. Host population size and geographic range of seabirds also correlate positively with the richness of their lice (Hughes and Page 2007).

Some former studies on parasite taxonomic richness have already treated host species richness as a potential confounding factor but found no association between them, possibly due to their relatively narrow host taxonomical range used (Felső and Rózsa 2006, 2007; Hughes and Page 2007). Nunn et al. (2004) found a positive correlation between primate diversification and richness of their viral and protozoan parasites; however, they used a different theoretical and statistical approach to analyze effects of host diversification rates (Agapow and Isaac 2002) rather than recent host diversity. Thus their results do not specifically refer to Eichler's rule (1942). No former studies directly examined the explanatory power of host taxonomic richness on parasite taxonomic richness by using modern methodologies.

The influence of host body mass on parasite taxonomic richness was described by several authors studying various

Table 1 An overview of louse suborders and families (Johnson and Clayton 2003), Anopluran families are not listed separately

	Families	Genera	Species	Hosts
Suborder Amblycera	6	95	1,334	Birds and mammals
Menoponidae		68	1,039	Birds
Boopiidae		8	55	Mammals[a]
Laemobothriidae		1	20	Birds
Ricinidae		3	109	Birds
Gyropidae		9	93	Mammals
Trimenoponidae		6	18	Mammals
Suborder Ischnocera	2	157	3,060	Birds and mammals
Philopteridae		138	2,698	Birds[a]
Trichodectidae		19	362	Mammals
Suborder Rhynchophthirina	1	1	3	Mammals
Suborder Anoplura	16	49	532	Mammals

[a] One louse species also occurs on the other class of hosts

host and parasite taxa. It is often presumed that larger-bodied host taxa may provide more diverse resources, say, more different types of spatial refuges to avoid host defenses. Alternatively, one could also predict a positive co-variation between host body size and parasite richness using the theory of island biogeography (Kuris et al. 1980). However, research on the interaction between host body size and parasite richness yielded contradictory results (see e.g. Poulin and Morand (2004), Poulin (2007) for reviews), suggesting that host body mass may not act as a general predictor of parasite diversity (Bordes et al. 2011; Hughes and Page 2007; Krasnov et al. 2004; Krasnov et al. 2008).

Here we aim to test Eichler's rule (Eichler 1942) on avian and mammalian lice. Our study incorporates all families of birds and mammals recognized by Dickinson (2003) and Bininda-Emonds et al. (2007), respectively. We also examine the relationship between host body mass and louse taxonomic richness on this broad data frame.

Materials and methods

Taxonomic richness of hosts and parasites

We examined variation in host traits at the family level. Avian and mammalian families form more or less well-recognized monophyletic clades according to recent molecular systematic studies, while higher level taxa do not prove to be monophyletic in many cases (Barker et al. 2004; Bininda-Emonds et al. 2007; Hackett et al. 2008). Phylogenetic comparisons require well-resolved trees, which are much more available at family level than for lower level taxa. Additionally, this level also helps accounting for missing information about louse presence at the species level, which is more complete at the family level.

We described species richness of all 175 avian families recognized by the Howard and Moore checklist (Dickinson 2003) and for all 147 mammalian family-level clades recognized by Bininda-Emonds et al. (2007). Host taxa involved in our analyses are summarized in Table 2 following Dickinson (2003), Perrins (2003), and Wilson and Reeder (2005). As species richness of host families varied considerably (see "Results") we log-transformed species richness data in all subsequent analyses. Although our results were nearly identical when we used raw species richness (not reported), we preferred to use the log-transformed data because they satisfied all the distributional assumptions of the statistical methods we adopted.

Table 2 A summary of host taxa involved in the analyses (Dickinson 2003; Perrins 2003; Wilson and Reeder 2005)

	Orders	Families	Genera	Species
Aves	28	175	2,051	9,320
Mammalia	29	147	1,131	4,616

A widely distributed bird species often hosts congeneric louse species each restricted to different and non-overlapping areas of the host distribution. Thus, parasite species richness of widely distributed bird species would overestimate the true parasite richness that each local bird population has to face (Clay 1964). Furthermore, taxonomists often use different species concepts to describe louse faunae (Mey 2003) making species richness an unreliable measure. Some taxonomists automatically described congeneric lice from different hosts as distinct species while other authors lump many species into a single one from a wide range of hosts (see Price (1975) as an example). Therefore, we used generic richness (i.e., the number of louse genera per host families) as a proxy of louse diversity.

Host–parasite associations and parasite generic richness values were obtained from the world checklist of chewing lice (Price et al. 2003) and sucking lice (Durden and Musser 1994). We collected data separately for louse suborders and, in the case of birds, also separately for each avian louse families. Apparently, these louse families are not only phylogenetically distinct but also exhibit marked ecological differences (Johnson and Clayton 2003). In case of mammals, it is not feasible to analyze families separately either because a suborder is represented by a single family (Ischnocera: Trichodectidae) or the families are rather taxon-poor (Amblyceran families) or because the families are ecologically homogeneous (Anopluran families). Therefore, we did not divide mammal lice into families in our analyses. We excluded Rhynchophthirina from the suborder-level analysis of mammalian lice and Boopiidae from the family-level analysis of avian lice, because they do not provide enough variability to justify a comparative analysis (Table 1).

Control for louse research effort

We controlled for uneven louse sampling effort in three different ways. Firstly, we used generic richness, which is less biased by sampling than species richness. Arguably, a larger proportion of louse species awaits description than louse genera (see e.g. Sychra et al. 2010).

Secondly, we calculated a study effort rate as the number of host species known to be associated with lice in a host family divided by the total number of species in that host family. We performed linear regressions using louse generic richness as a response variable and study effort rate as an explanatory variable. We obtained the residuals from these linear regression models and used them in the subsequent analyses. This is a widespread method in comparative studies to control for confounding variables (Garland et al. 1992), even though it can sometimes cause bias (Freckleton 2009), particularly when the explanatory variables are correlated (Freckleton 2002), as in the case of study research effort rate and host species richness. By using this residual analysis method, we may overestimate the effect of sampling effort and underestimate the effect of host species richness on louse generic richness (Freckleton 2002).

Finally, in the avian dataset we excluded all families for which no louse species had been recorded (e.g., Balaenicipitidae and Todidae) and in the mammalian dataset all orders without lice (e.g., Cetacea and Chiroptera). Naturally, this reduced sample sizes.

As the results in the subsequent analyses were identical when any of these three ways to control for uneven sampling effort were used (see only one exception in "Results"), we report only the analysis based on the raw generic richness.

Average body mass of host families

We quantified the average body mass of each family in two different ways. Firstly, we took body mass data available for 129 avian families from Perrins (2003) and for all mammalian families from Nowak (1999) and Macdonald (2001). Values were obtained simply by averaging the minimum and maximum values in each family. However, calculating family body mass by averaging the minimum and maximum values may lead to bias, given that the distribution of body masses among species within a family is not even but skewed. Therefore, we also assessed family-level averages by randomly sampling five species from each family using the "sample" function in R 2.11.1 (R Development Core Team 2010) and averaged their body masses obtained from Dunning (2008) for birds and Silva and Downing (1995) for mammals. Families below five species were represented by all available data. Averages were log-transformed in all subsequent analyses. As the results in the subsequent analyses were qualitatively identical when any of these two measures were applied (see only one exception in Results), we report only the analysis based on the latter body size estimate.

Phylogenetic trees

To take the evolutionary history into account (Felsenstein 1985, 2004), we constructed a phylogenetic tree of avian families based on Barker et al. (2004) and Hackett et al. (2008). The non-passerine branching pattern from Hackett et al. (2008) was combined with passerine topology from Barker et al. (2004). Naturally, we lost branch length data this way; however, arbitrary branch lengths were calculated using Nee's method (Purvis 1995), as this method provided the best fit according to the most widespread and reliable diagnostic plots recommended by several methodological studies (Diaz-Uriarte and Garland 1996, 1998; Garland et al. 1992).

The phylogenetic relationships of mammalian families were based on a family-level tree published by Bininda-Emonds et al. (2007). Branch length data (proportional to time) were also obtained from the same source. If the family-level clades were different from those accepted by Wilson and Reeder (2005), their taxonomic content was determined using the supplemental information of Bininda-Emonds et al. (2008: Suppl. Fig. 1) (e.g. Geomyidae 1=*Thomomys*, Geomyidae 2=*Geomys*, Geomyidae 3=*Pappogeomys*, Geomyidae 4=*Orthogeomys* and *Zygogeomys*) and louse generic richness and body mass data were corrected accordingly.

As the phylogenetic trees contained some polytomies reflecting the uncertainty of bifurcating patterns, we used the method of bounded degrees of freedom, as recommended by Purvis and Garland (1993) and tested by Garland and Díaz-Uriarte (1999), to avoid inflation of type I errors in the comparative analysis.

We constructed the phylogenetic trees in Mesquite 2.74 (Maddison and Maddison 2010). Basic diagnostic plots, arbitrary branch length transformations, and the method of bounded degrees of freedom are also implemented in this software.

Statistical analysis

We controlled for the statistical non-independence of traits of related taxa by using the method of independent contrasts (Felsenstein 1985). These calculations were carried out with PDAP: PDTREE 1.15 module (Midford et al. 2010) in Mesquite (Maddison and Maddison 2010). Character evolution was simulated under a Brownian motion model (Felsenstein 1985). Although this model may not represent perfectly the process of evolutionary changes, several authors showed that even with errors in branch lengths and deviations from Brownian motion the method of independent contrasts is robust and reliable (Diaz-Uriarte and Garland 1996, 1998).

Only two continuous variables can be tested simultaneously by using the method of independent contrasts in Mesquite (Maddison and Maddison 2010). Therefore, in cases when more than one variable had a significant effect on a response variable, we created standardized contrasts and performed multiple linear regressions to test the explanatory power of all variables on the louse taxonomic richness at the same time. All regressions were forced through the origin (Felsenstein 1985; Garland et al. 1992). We checked for multicollinearity between the explanatory variables by variance inflation factor (VIF) (Reiczigel et al. 2007). These analyses were carried out with R 2.11.1 (R Development Core Team 2010) using the package "faraway" (Faraway 2009). The distributional assumptions of the statistical tests used were checked graphically (e.g., quantile-comparison plot). All analyses were two-tailed.

Results

Mean species richness of avian families was 53.3 (range, 1–400), while mean species richness of mammalian families was 31.4 (range, 1–1,326). The mean generic richness of lice (whole Phthiraptera) was 3.6 (range, 0–20) on avian families, and 1.2 (range, 0–11) on mammalian families.

We investigated whether species richness of host families predicts generic richness of lice. Louse richness values were taken as response variables, while host richness acted as the explanatory variable. In the avian dataset, we found significant positive relationships between host species richness and the generic richness of the whole order (Fig. 1), both suborders and all families of lice, except Laemobothriidae (Table 3). This latter non-significant correlation acted as the only difference in the results of the datasets controlled for louse sampling effort in three different ways (see "Materials and methods"). This correlation was significant neither when raw generic richness data was used nor when families without louse associations were excluded. However, by residual analysis we found a weak positive correlation (p=0.042). In the mammalian dataset, we found significant positive relationships between host species richness and the generic richness of the whole order (Fig. 2) and all investigated suborders of lice (Table 3).

We also checked whether host body mass predicts louse generic richness. In the avian dataset we found that generic richness of Ricinidae co-varied negatively with host body mass, while no relationship appeared with other louse taxa (Table 4). However, in case of Menoponids results differed according to different body mass measures. When estimating family body masses by averaging the minimum and maximum values (see "Materials and methods"), we found a marginally significant positive correlation (p=0.049) between body mass and Menoponid richness. However, even in this case body mass failed to show a significant effect on Menoponid richness in a multiple linear regression model. Body mass of mammals did not predict the generic richness of any of the louse taxa (Table 4).

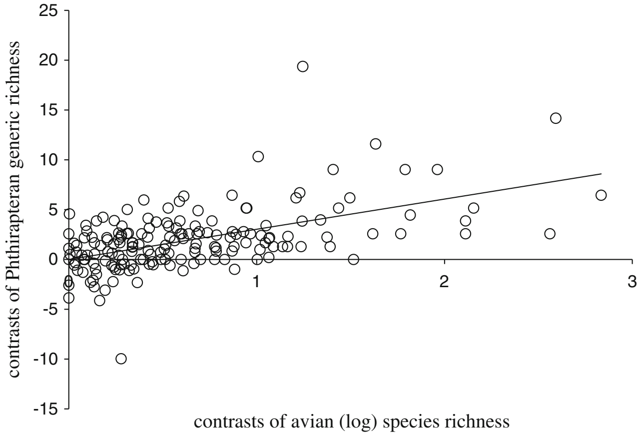

Fig. 1 Regression between contrasts of avian (log) species richness and contrasts of Phthirapteran generic richness

Table 3 Results of linear regression between contrasts of (log) host species richness and contrasts of louse generic richness

	Slope	R^2	F value	p value
Avian families (n=174; df=172)				
Phthiraptera	3.03	0.48	158.62	<0.001
Ischnocera: Philopteridae	1.75	0.34	89.84	<0.001
Amblycera	1.28	0.46	149.54	<0.001
Amblycera: Menoponidae	1.06	0.38	103.98	<0.001
Amblycera: Ricinidae	0.19	0.11	21.50	<0.001
Amblycera: Laemobothriidae	0.04	0.01	2.14	0.146
Mammalian families (n=146; df=128)				
Phthiraptera	1.53	0.29	58.27	<0.001
Ischnocera	0.30	0.08	11.86	<0.001
Amblycera	0.45	0.11	17.16	<0.001
Anoplura	0.78	0.20	37.09	<0.001

In the case of Ricinids, both host species richness (Table 3) and body mass (Table 4) had a significant effect on the richness of lice. We therefore performed multiple linear regressions with the standardized contrasts, forced through the origin. Ricinid generic richness co-varied significantly both with host species richness (slope=0.17, p< 0.001) and body mass (slope=−0.16, p=0.006, $F_{(2,172)}$=15, adjusted R^2=0.14). There was no multicollinearity between these explanatory variables (VIF value=1.02).

Discussion

Several recent studies (see e.g. Krasnov 2008) on the environmental correlates of parasite diversity used a "diversity concept" different from the "richness concept" used here. They considered not only the number of parasite taxa, but also a taxonomical distinctness of these taxa as components of parasite diversity. Here we did not follow this line due to three reasons. Firstly, Eichler's (1942) original hypothesis referred only to the numbers of host and parasite taxa within an assemblage, and not to their distinctness. Secondly, we had no branch length data for the parasite phylogeny, thus we could use only the systematical hierarchy to assess taxonomical distinctness in the sense of Warwick and Clarke's (1995)—a rough method based on unrealistic presumptions. Finally, if we use the number and distinctness of parasite taxa to quantify the diversity of a parasite assemblage, then we should use the

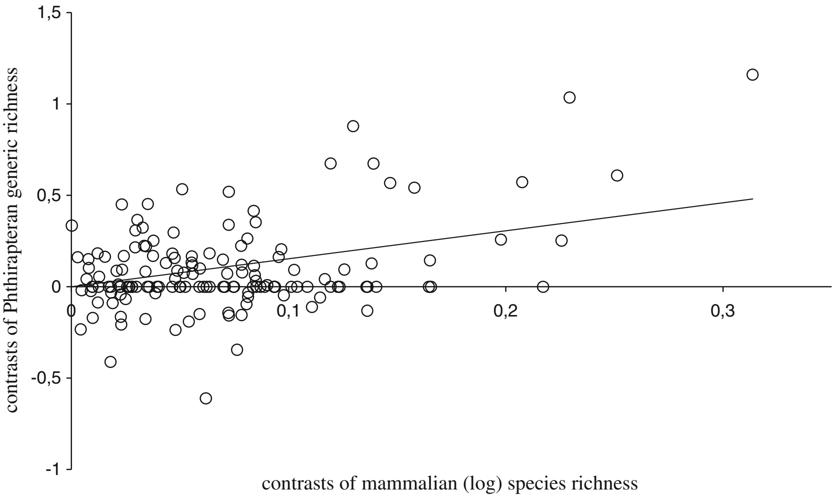

Fig. 2 Regression between contrasts of mammalian (log) species richness and contrasts of Phthirapteran generic richness

same approach to quantify host diversity as well—a source of substantial further complications.

Thus, for sake of simplicity, we tested strictly what Eichler predicted—i.e., the positive co-variation between the richness of host and parasite taxa and we found strong support for Eichler's rule.

The biological interpretation of louse generic richness—our measure of parasite richness—is quite straightforward. Co-existing lice taxa exhibit quite distinct body size and body shape differences according to the specific microhabitats they occupy on a particular host species (Johnson and Clayton 2003). Therefore, different louse genera can roughly be interpreted as different ecological guilds utilizing different environmental resources (such as refuges to avoid host defenses) in the sense of Simberloff and Dayan (1991).

The taxonomic richness of avian families showed a significant positive correlation with the generic richness of the whole order of lice (Fig. 1), both suborders and three out of four families of lice (Table 3). To the best of our knowledge, only one former study (Hughes and Page 2007) succeeded in finding any trait that co-varies with Ischnoceran taxonomic richness showing that population size co-varies positively with Ischnoceran species richness. On the contrary, however, several traits studied by previous authors showed a significant relationship with Amblyceran taxonomic richness and no relationships with Ischnocerans (Clayton and Walther 2001; Hughes and Page 2007; Møller and Rózsa 2005; Møller et al. 2010; Vas et al. 2011). The generic richness of Laemobothriidae, not surprisingly, failed to co-vary significantly with host taxonomic richness, as this family contains only one genus and has an erratic and still unexplained distribution pattern among birds. They infest several species of Ciconiiformes, Gruiformes, Falconiformes, and Strigiformes (Price et al. 2003), though the latter may well be an erroneous host record.

Table 4 Results of linear regression between contrasts of (log) host body mass and contrasts of louse generic richness

	Slope	R^2	*F* value	*p* value
Avian families (n=174; df=172)				
Phthiraptera	−0.33	<0.01	0.48	0.490
Ischnocera: Philopteridae	−0.14	<0.01	0.19	0.660
Amblycera	−0.19	<0.01	0.83	0.468
Amblycera: Menoponidae	<0.01	<0.01	<0.01	0.987
Amblycera: Ricinidae	−0.19	0.05	10.06	0.002
Amblycera: Laemobothriidae	−0.02	<0.01	0.29	0.591
Mammalian families (n=116; df=98)				
Phthiraptera	−0.37	0.02	2.94	0.090
Ischnocera	−0.09	0.01	1.14	0.288
Amblycera	−0.08	<0.01	0.57	0.452
Anoplura	−0.23	0.02	2.94	0.089

Host species richness of mammalian families co-varied positively with the generic richness of the whole order and all investigated suborders of Phthiraptera (Table 3).

Several explanatory powers (R^2 values) reported in Table 3 are unusually high in comparison with other comparative studies in evolutionary ecology, in which R^2 values were found frequently in the range 0.05–0.10 (Freckleton 2009). However, R^2 values reported here range up to 0.48, reflecting an exceptionally high explanatory power, and strong support for Eichler (1942).

What evolutionary and ecological progresses are behind Eichler's rule? Why do taxon-rich host clades harbor more diverse parasite faunae? Below we propose some alternative hypotheses that may explain the strong correlation between host and parasite taxonomic richness. These hypotheses may not be mutually exclusive, and partly based on former arguments of Eichler (1942), Nunn et al. (2004), and Hughes and Page (2007).

Firstly, from a macroevolutionary viewpoint, the most obvious answer lies in host–parasite cospeciation. In a speciation event of hosts the possibility of horizontal gene transfer breaks not only between host populations but often also between parasite populations infesting them. Reproductive isolation of hosts reduces physical contacts that are often crucial for parasite transmission (Johnson and Clayton 2003). Presuming high host specificity, we expect host and parasite speciation to follow each other (Page 2003). Given these conditions, taxon-rich host clades would be infested with a taxon-rich parasite fauna, as compared to host clades with little branching (Eichler 1942). However, contrary to early expectations (Fahrenholz 1913), parasites often do not significantly cospeciate with their hosts (see Page (2003) for a review). Indeed, cospeciation events seem to be about as frequent in lice as in any other group of parasites (Page 2003).

One can reasonably change the direction of causality by presuming that parasite richness forces host taxa to increase speciation. Indeed, pathogen taxonomical diversity is an important determinant of selection pressure exerted by parasites (Bordes and Morand 2009), which may increase host speciation through processes such as parasite-mediated sexual selection. These two directions are not mutually excluding each other. Presuming that high parasite richness can increase host diversity and then host diversity can also facilitate subsequent parasite speciation may lead us to hypothesize an autocatalytic process resulting a coevolutionary increase of richness in certain host–parasite lineages.

Secondly, from a macroecological viewpoint, host population size and geographic range may also influence avian (Gregory 1990; Hughes and Page 2007) and mammalian (Poulin 2007) parasite diversity. Species-rich host clades may occupy greater area and more diverse habitats, and they may also incorporate a larger number of individuals; hence they have a greater chance of coming into contact with other species. Thus they are more exposed to host switching parasites (Gregory 1990; Hughes and Page 2007; Nunn et al. 2004). This phenomenon may also contribute to the correlation described above.

On the contrary, one could reasonably argue that host taxonomic richness may affect parasite extinction rates rather than speciation rates. Lice—just like many other parasites—exhibit relatively strict host specificity with rare and accidental host-switches during their evolutionary history. The chance of a successful host-switch is likely to be higher if the donor and the recipient host species are closely related phylogenetically and, therefore, morphologically. Arguably, louse taxa parasitizing species-rich host clades are less prone to extinction simply because they have a higher chance to establish parallel populations harbored by different host species. This phenomenon may contribute to the apparent lack of lice on taxon-poor host families like Balaenicipitidae, Rhynochetidae, or Todidae.

In the wide taxonomic range presented by this study, host body mass does not seem a key factor shaping louse richness, as is also suggested by several earlier studies (Bordes et al. 2011; Hughes and Page 2007; Krasnov et al. 2004; Krasnov et al. 2008; Poulin 2007). We found, however, that body mass had a strong effect on the generic richness of Ricinids. This is not surprising, given the fact that members of this family infest only hummingbirds and small-bodied passerines (Price et al. 2003). Ricinids are considerably large themselves (Nelson 1972; Rheinwald 1968), hence the factors shaping their peculiar host distribution need further study. Host body mass appears to be more important in shaping other measures of louse infestations, such as prevalence and intensity (Rózsa 1997a, b). However, as it is harder to obtain these kinds of data properly, little is known about how body mass affects infestation measures on a broad phylogenetic scale.

We conclude that exceptionally strong correlational evidence supports the positive co-variation between the species richness of avian and mammalian families and the generic richness of their lice. Given the fact that this relationship is highly significant across all major host and parasite taxa involved in the present study, we propose that it may well be a quite general feature of parasitism and likely also of other historical associations like mutualism. The generality of this phenomenon is also supported by the recent finding that lice represent two independent origins of parasitism (Johnson et al. 2004; Murrell and Barker 2005; Smith et al. 2011). Whatever the driving force and the exact mechanism beyond this phenomenon is, it seems possible that it may greatly contribute to the global biodiversity. Further studies should test the validity of Eichler's rule on a wider range of hosts, parasites, and mutualists, and also at other levels of the taxonomical hierarchy.

Acknowledgments We are grateful to Dr. Olaf R. P. Bininda-Emonds for kindly sending us a nexus format of their family-level mammalian tree. We thank Anikó Kovács-Hostyánszki for translating German papers. We would like to express our gratitude to Dr. Thomas Cooper (Eszterházy Károly College, Dept. of American Studies) for the linguistic corrections.

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