Parasite extinction and colonisation and the evolution of parasite communities: a simulation study

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Abstract

We determined what evolutionary processes influence the likelihood of detecting an effect of host ecological characteristics on the richness of parasite communities in comparative analyses among related host species. We used a mathematical model to generate phylogenies of hosts in which parasite communities varied over evolutionary time as parasite species were either gained or lost during host speciation events. Gain or loss of parasites were stochastic and could either be strongly, moderately, weakly, or not, affected by host ecological characteristics. The model was evaluated over this range of effects of host ecology, and for various mean probabilities of parasite gain and loss and various rates of change in host ecological characteristics at speciation events. Our results suggest that phylogenetic effects (the passing of parasite species from mother to daughter host species) are likely to obscure ecological effects (the effect of host body size, diet, habitat, lifespan, etc.) except when the effects of host ecology are strong, and the probabilities of gain or loss of parasites are high, or host ecological characteristics change markedly at speciation events. This outcome was not influenced by the shape of the phylogenetic tree used in the simulations. Sensitivity analysis of our model also shows this result to be robust to a wide range of assumptions and parameter values. Thus, because the composition of parasite communities tends to reflect their ancestry, the effect of host ecology will often be very difficult to detect. © 1998 Australian Society for Parasitology. Published by Elsevier Science Ltd.

Key words: Colonisation; Comparative analyses; Computer simulations; Extinction; Parasite communities; Phylogenetic effects

1. Introduction

Contemporary species assemblages reflect both a legacy of historical contingencies and the recent action of ecological processes [1, 2]. The relative importance of these two determinants of community structure is the subject of some debate, especially among students of parasite communities [3, 4]. Much effort has gone recently into linking the interspecific variability in richness and diversity of parasite faunas with host ecology, in many taxa of vertebrate hosts [5–7]. The use of island biogeography theory has played a key role in the development of parasite community ecology [8]; however, there are important differences between insular habitats and hosts. Different parasite communities occupy habitats (hosts) whose historical origins may be linked, and undergo evolutionary changes that may reflect the history (phylogeny) of those habitats. For instance, when allopatric spe-

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ciation occurs in a host lineage, the resulting daughter host species are likely to harbor very similar parasite communities; the degree of similarity between the parasite faunas of two host species may then mirror their relatedness. A form of evolutionary inertia should result in many if not most parasite species in a community being inherited from an ancestral host rather than being newly acquired. The potential importance of history, or phylogeny, in the evolution of parasite communities appears clear. However, attempts at explaining the structure of parasite communities rely almost solely on ecological differences among host species (see studies listed above), or invoke chance events and view parasite communities as mostly stochastic assemblages [9, 10].

There is no doubt that host ecology plays a role in structuring parasite communities. Traits such as host body size, longevity, diet breadth, and geographical range often correlate positively with parasite richness across host species. However, at least some of these patterns may be artefacts of uncontrolled phylogenetic effects [11, 12]. Recent comparative analyses, which used phylogenetically independent contrasts, revealed no association between body size and the richness of the gastrointestinal parasite community among bird and mammal hosts, whereas analyses across species not controlling for phylogeny had found strong relationships between the two variables [11, 13]. Thus, contemporary parasite communities are inherited from ancestral hosts with some modifications, and to study how host ecological characteristics may have influenced these modifications without considering the relatedness among hosts can be very misleading. This fact is not emphasised strongly enough in recent reviews on parasite community ecology [14, 15].

A complete picture of the evolution of parasite communities would require information not only about host phylogeny, but also about the parasite communities of extinct hosts; the latter information is unavailable. In this paper, we first review the different ways in which the species composition of parasite communities can change through evolutionary time. We then use computer simulations to evaluate how common these changes in parasite communities must be, and how strongly linked to host ecological characteristics they must be, for this link to be detectable after phylogenetic influences are removed. Our objective is not to assess the relative importance of phylogeny and ecology, but to highlight the difficulties of properly evaluating the role of ecology in the evolution of parasite communities. The simulations recreate the evolution of an ancestral parasite community through the phylogenetic history of its host. Their results provide an insight into the nature of the mosaics of inherited, acquired, and lost parasites that are contemporary parasite communities.

2. Evolutionary events and parasite communities

Whereas the population structure of any parasite species results from the interaction of several ecological processes, the mere presence of that parasite in a host is an evolutionary phenomenon [16]. Several evolutionary events will result in either the loss or the acquisition of parasite species by hosts. These have been discussed by researchers attempting to reconstruct and compare host and parasite phylogenies [17, 18], and they are graphically illustrated in Fig. 1. In most cases, parasites are likely to be inherited from ancestral hosts, i.e. parasites of a host are passed down to daughter host species during host speciation, e.g. parasite B in Fig. 1. The inheritance of parasite species can be viewed as a null model of host–parasite coevolution. The parasite may or may not cospeciate with the host at that point; here, we deal with parasite lineages rather than with parasite species, and will not worry about the possibility of parasite speciation. The presence of inherited parasites in the parasite community of a host species is the result of phylogenetic inertia, and has nothing to do with the ecological changes undergone by the host.

Parasites can be lost in two general ways [17, 18]. First, a parasite lineage may go extinct in a host lineage (e.g. parasite A in host 1, in Fig. 1). Parasite extinction may be caused by several factors. For example, the host may become resistant, the parasite may be displaced by colonising parasite species, other host species necessary for the completion of the parasite's life cycle may disappear, or environmental changes may lead to inhospitable conditions
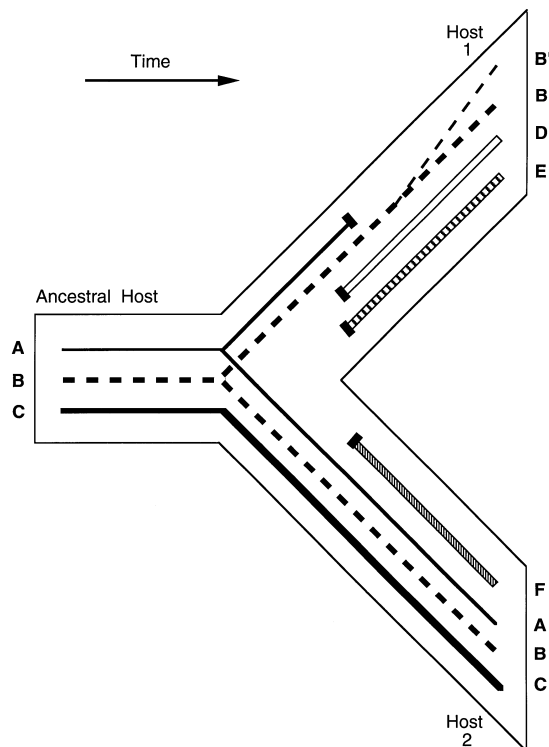
Fig. 1. Summary of evolutionary events leading to the diversification of parasite communities. Parasite lineages A to F are represented by different lines within the branching host lineage. Details are provided in the text.

for the free-living stages of the parasite. Second, it is possible that the part of the ancestral host population which gave rise to a new host species did not contain parasites during the speciation event, e.g. parasite C not present at the base of the branch leading to host 1, in Fig. 1. Typically, most hosts in a population harbor few or no parasites, most parasites being concentrated in/on a minority of hosts [19, 20]; parasites may thus be absent from a founder host population, or present in such small numbers that they quickly disappear. Whether parasites fail to join a founder population, or do so only to later become extinct, does not matter much: in either case a parasite lineage is lost. In fact, the two processes by which parasites are lost, though distinct, are probably not distinguishable because they differ mainly in timing.

There are also two ways in which new parasites can be acquired by hosts [17, 18]. First, hosts can be colonised by new parasite species, e.g. parasites D and E in host 1 and parasite F in host 2, in Fig. 1. These can transfer to new hosts from sympatric host lineages, provided that the new hosts are immunologically, physiologically, and ecologically compatible with the parasites. The second way in which new parasites can be acquired by hosts involves intra-host parasite speciation (parasite B splitting into parasites B and B′ in host 1, in Fig. 1). It can sometimes be a common phenomenon [18] and is one explanation for the occurrence of congeneric parasite species in the same host species. In this paper, we do not differentiate between the two mechanisms.

Loss and acquisition of parasites during evolutionary time may be rare events, much rarer than implied by the hypothetical example of Fig. 1 in which two hosts issued from a common immediate ancestor display very different parasite communities. The likelihood of losing or acquiring parasites may be related to the ecological characteristics of the host lineages. Following a speciation event, newly-formed host lineages may diverge with respect to body size, diet breadth or geographical range, all traits which may be linked with the probability of losing or gaining parasites. For instance, hosts with varied diets or large geographical ranges may frequently come into contact with new types of parasites and experience higher rates of successful colonisation than hosts with more restricted diets and ranges. Larger-bodied hosts may offer more space and perhaps a greater variety of niches for parasites, making colonisation and intra-host parasite speciation more likely than in small-bodied hosts. Similarly, a large host geographical range may compensate for local parasite disappearance and make parasite extinction from a host lineage less likely. Therefore, the extent to which parasite communities will change through the phylogenetic evolution of host lineages will depend at least in part on the ecological characteristics of the hosts.

3. Simulation procedures

The simulations were performed using a program written in Basic and available from the first author. They all begin with a single ancestral host species,

which then undergoes four rounds of speciation, i.e. the ancestor and its descendants each split into two new species during each round. This results in 16 host species at the tips of a phylogenetic tree involving 15 separate speciation events. The timing of speciation events during each round is synchronised to produce a balanced, symmetric tree with all branches equal in length. Note that this could simulate the evolutionary history of 16 different host species as well as that of 16 distinct populations of the same host species. We performed further simulations to make sure that our results did not depend on the shape of the tree used. In those simulations, we used a fully pectinate tree instead of a balanced tree.

In each simulation, a pool of 16 parasite species is originally defined and remains constant throughout. Although referred to as species, these parasites may best be viewed as lineages since in reality they could cospeciate with their hosts. The ancestral host harboured six parasite species from that pool of 16. At each host speciation event, each parasite species harbored in the parent host species has a basic probability, P, of being lost by either of the two newly-formed host species. At the same time, all parasite species not currently harbored have an equal basic probability, q, of being acquired by (or of colonising) the newly-formed host species.

The probabilities P and q, however, will be influenced by the ecological characteristics of the newly-formed host species. We defined a variable called host ecology, or H, and gave it a value of 0 in the ancestral host species. This variable could represent any quantitative ecological trait of the host likely to affect parasite acquisition and extinction, such as body mass, geographical range, or diet breadth. At each speciation event, the host ecology value of each of the newly-formed species can differ from that of the parent species, varying according to a normal probability distribution with mean zero and a specified standard deviation (referred to as S.D.). Depending on how strongly parasite acquisition and extinction are linked to host ecology, the probabilities P and q can be strongly, weakly, or not at all influenced by host ecology. In order to obtain actual probabilities of extinction and colonisation at each host speciation event ($P*$ and $q*$, respectively), we related P and q to H as follows:

$$P* = 2Pe^{-Hf}/(1 + e^{-Hf})$$

$$q* = 2qe^{Hf}/(1 + e^{Hf})$$

where e is the base of natural logarithms and f is a coefficient determining the effect of H. When f equals zero, host ecology has no effect on parasite extinction or colonisation, and the effect of host ecology increases as the value of f increases. The above equations are arbitrary constructs that could no doubt be substituted with other formulae; they are only meant to provide a statistical link between host ecology and the rates of parasite extinction or acquisition. In the simulations, we considered four scenarios: $f = 0$ (H has no effect, with $P* = P$ and $q* = q$), $f = 0.5$ (H has a weak effect), $f = 1$ (H has a moderate effect), and $f = 2$ (H has a strong effect, resulting in $P*$ and $q*$ values often more than double the basic rates P and q).

For each of the four above scenarios, and for each combination of the three parameters we varied (P, q, and the S.D. of change in host ecology or S.D.), we performed 10 000 simulations. The probabilities P and q were given values ranging from 0.0005 to 0.35, whereas S.D. varied between 0.1 and 5. At the end of each simulation, correlations between parasite richness and host ecology were computed in two ways. First, simple correlations were calculated among the 16 "living" host species, i.e. the 16 species at the branch tips of the phylogenetic tree. Second, in order to control for phylogenetic effects and the simple inheritance of parasite species unrelated to changes in host ecology, we computed contrasts between pairs of branches issued from each of the 15 speciation events in the tree. In other words, we calculated the differences in both parasite richness and host ecology between the 15 pairs of sister host species in the phylogeny, and used these phylogenetically-independent differences in correlation analyses. Data points are therefore independent measures of divergence in the two variables and not actual species values. This method is the most widely used technique to control for phylogenetic influences [21]. It does not allow the magnitude of phylogenetic influences to be evaluated, but it allows the effect of host ecology to be measured free of any phylogenetic influences. We computed correlations, forced through the origin [22], among the phylogenetic contrasts. The

independent contrast method provides a valid and powerful test of the relationship between two variables when the phylogeny is fully resolved and true branch lengths are known [23], as in this case. Values for these two types of correlations were averaged across all 10 000 simulations in each series, and used as measures of the association between host ecology and parasite species richness.

To evaluate the robustness of the results, we conducted a sensitivity analysis by doing further simulations varying parameters that had been kept constant in the series described above. We changed the number of parasite species in the pool, the number of parasite species present in the ancestral host species, the number of speciation rounds per simulation, and the process of parasite acquisition and loss.

4. Results

Simple correlations computed across the host species from the tips of branches generally gave results similar to those obtained with correlations across independent contrasts, with two important differences. First, when we specified no relationship between host ecology and the probabilities of both parasite extinction and colonisation, i.e. $f=0$, the cross-species correlations between host ecology and parasite species richness were significant twice as often as expected by chance. For instance, with $\alpha=0.05$, we typically obtained significant correlations in about 10% of simulations in a series. No such high rate of type I error was observed with correlations among contrasts. Second, when both parasite extinction and colonisation were functions of host ecology, i.e. $f>0$, cross-species correlations were more powerful at detecting the relationship between parasite species richness and host ecology than were correlations among contrasts, and the values of cross-species correlation coefficients were typically much higher. The likelihood of a type II error thus appears greater when using correlations among contrasts. However, because of the bias in tests of the cross-species correlation (see also Purvis et al. [23]), we only present results obtained using correlations among contrasts.

The simulations indicate that parasite extinction

(Fig. 2) or colonisation of new hosts (Fig. 3) need to be relatively frequent events in the phylogenetic history of hosts for the relationship between host ecology and parasite species richness to be statistically detectable. Only when either or both P and q values are high is the relationship likely to be
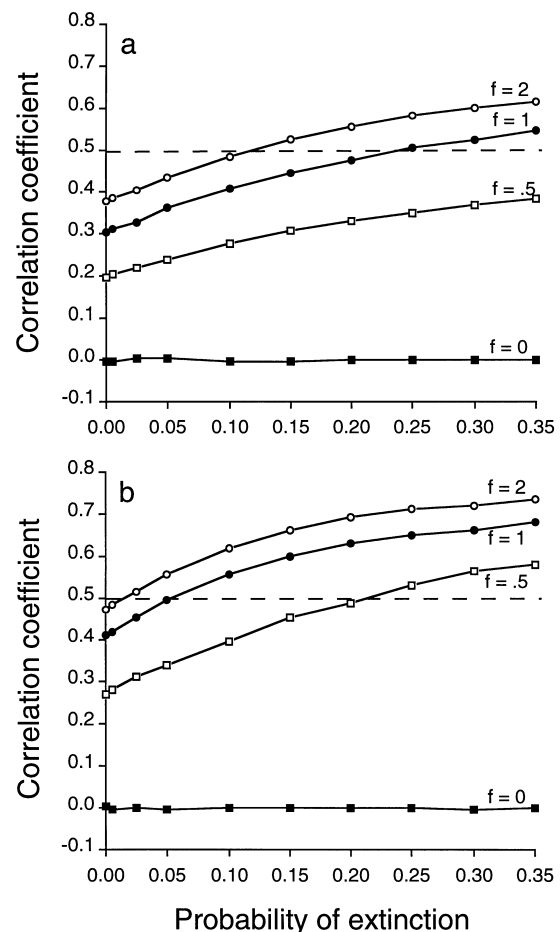

Fig. 2. Plot of the strength of the relationship between host ecology and parasite species richness, as a function of the basic probability of parasite extinction following host speciation events, P, when $q=0.1$ (a) and $q=0.3$ (b). The relationship between host ecology and parasite species richness was assessed with a correlation forced through the origin using phylogenetically independent contrasts. Results are presented separately for different values of f, the coefficient determining the strength of the effect of host ecology on P^* and q^*. Each point is the average of correlation coefficients obtained from 10 000 separate simulations. The broken line represents the critical value ($\alpha=0.05$) of the correlation coefficient for 15 contrasts (d.f. = 14). The other parameter, S.D., was kept constant at 1.
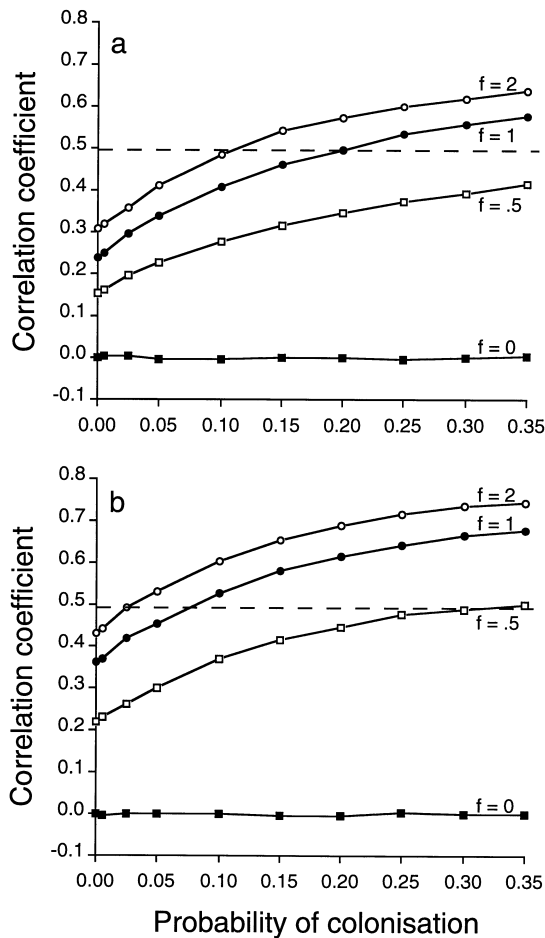
Fig. 3. Plot of the strength of the relationship between host ecology and parasite species richness, as a function of the basic probability of parasite colonisation following host speciation events, q, when $P=0.1$ (a) and $P=0.3$ (b). The relationship between host ecology and parasite species richness was assessed with a correlation forced through the origin using phylogenetically independent contrasts. Results are presented separately for different values of f, the coefficient determining the strength of the effect of host ecology on P^* and q^*. Each point is the average of correlation coefficients obtained from 10 000 separate simulations. The broken line represents the critical value ($\alpha=0.05$) of the correlation coefficient for 15 contrasts (d.f. = 14). The other parameter, S.D., was kept constant at 1.

found. This is true even when the association between host ecology and parasite loss and acquisition is a strong one, i.e. $f=2$. Weak coupling between host ecology and parasite loss and acqui-

sition, i.e. $f=0.5$, can make any relationship impossible to detect (see Table 1).

The magnitude of changes in host ecology during branching events is also important (Fig. 4). As daughter host species are allowed to depart more from the host ecology value of their immediate ancestor, the relationship between host ecology and parasite species richness strengthens. This effect disappears at high values of S.D., where further variability in changes in host ecology have no additional influence on the relationship between host ecology and parasite species richness (Fig. 4).

The above results are derived from simulations using a balanced host phylogeny. When using a fully pectinate host tree, i.e. an extremely unbalanced tree, we obtained identical trends except that the values of correlation coefficients were always slightly lower than the corresponding values from the original simulations using balanced trees. Since branch lengths in the pectinate tree were not all equal, the speciational model of evolutionary change used in the previous analyses may have been inappropriate. Adjusting the model so that change in host ecology and gain or loss of parasites became proportional to branch length gave correlation coefficients that were generally slightly higher. The detection of a relationship between host ecology and parasite species richness, however, remained possible only when the rates of species gain or loss were high and when changes in host ecology at branching events are large enough.

The sensitivity analysis, repeating the simulations with balanced trees while varying values of parameters held constant in the initial analyses, shows that our results are quite robust over a wide range of assumptions (Table 1). We increased the number of parasite species in the pool from 16 to 64, and found that this change had no measurable impact on the results of the simulations. Then, using again a pool of 16 parasite species, we began with an ancestral host harbouring two instead of six species. The results of these simulations were similar to those reported above, except that slightly lower correlation coefficients between host ecology and parasite species richness were obtained for low values of q, the probability of parasite colonisation. Clearly, this is expected when acquisition of species is constrained and the initial parasite community is depa-

Table 1
Simulation conditions and power of the correlation analysis to detect a relationship between parasite species richness and host ecology*

Number of species in parasite pool				16	64	16	16	infinite	infinite
Number of parasites in ancestral host				6	6	6	2	6	6
Number of rounds of speciation				4	4	5	4	4	6
Multiple gains or losses?				yes	yes	yes	yes	no	no
P	q	S.D.	f						
0.0005	0.1	1	0.5	0.19	0.20	0.27	0.23	0.08	0.13
0.0005	0.1	1	1	0.33	0.34	0.48	0.41	0.10	0.19
0.0005	0.1	1	2	0.46	0.46	0.63	0.56	0.12	0.24
0.1	0.1	1	0.5	0.29	0.29	0.47	0.28	0.09	0.18
0.1	0.1	1	1	0.52	0.51	0.74	0.51	0.14	0.27
0.1	0.1	1	2	0.66	0.66	0.86	0.67	0.17	0.36
0.1	0.0005	1	0.5	0.14	0.15	0.20	0.10	0.08	0.13
0.1	0.0005	1	1	0.24	0.24	0.35	0.13	0.10	0.19
0.1	0.0005	1	2	0.34	0.35	0.49	0.18	0.12	0.24
0.1	0.1	.1	0.5	0.07	0.07	0.07	0.06	0.06	0.06
0.1	0.1	.1	1	0.08	0.08	0.10	0.08	0.06	0.07
0.1	0.1	.1	2	0.12	0.12	0.18	0.12	0.07	0.10
0.1	0.1	5	0.5	0.67	0.68	0.86	0.69	0.17	0.38
0.1	0.1	5	1	0.69	0.68	0.86	0.68	0.19	0.40
0.1	0.1	5	2	0.66	0.66	0.84	0.67	0.20	0.40

* Simulations were performed for different values of P (the probability of parasite extinction at each speciation event), q (the probability of a new parasite being acquired at each speciation event), S.D. (the standard deviation of change in host ecology), and f (the coefficient determining the strength of the effect of host ecology on P and q).

uperate. Next, we went back to six parasite species (from a pool of 16) present in the ancestral host, but we added one round of speciation to the phylogeny in the simulations, ending up with 32 host species rather than only 16 at the branch tips of the tree. Essentially identical results as those described earlier were obtained. However, although the values of the correlation coefficients were the same, the greater number of degrees of freedom in the correlation analysis resulted in a lower critical value, i.e. a lowering of the broken line in Figs 2–4, so that the analysis was more likely to produce significant relationships between host ecology and parasite species richness (Table 1). Finally, we changed the parasite acquisition and loss process by assuming an infinite pool of possible additions, but limiting the host to a possible gain or loss of only one parasite per host speciation. This produced the same pattern as our initial simulations (with a parasite pool of only 16 species and possible multiple acquisitions or losses), but correlation coefficients were substantially (60–70%) lower. This resulted in substantially lower power to detect relationships between parasite species richness and host ecology (Table 1). The lack of power (compared with the initial simulations) persisted even when the latter simulations were extended to six rounds of speciation (64 host species at the tips of branches in the phylogenetic tree), thus greatly increasing the number of degrees of freedom (Table 1).

5. Discussion

Although the rigorous study of parasite community ecology has flourished in the past 2 decades, attempts to distinguish between phylogenetic/historical and ecological influences are only very recent [5, 11, 12, 24]. The relative importance of host phylogeny and ecology in determining parasite community richness is difficult to assess without a complete fossil record of ancestral parasite assem-
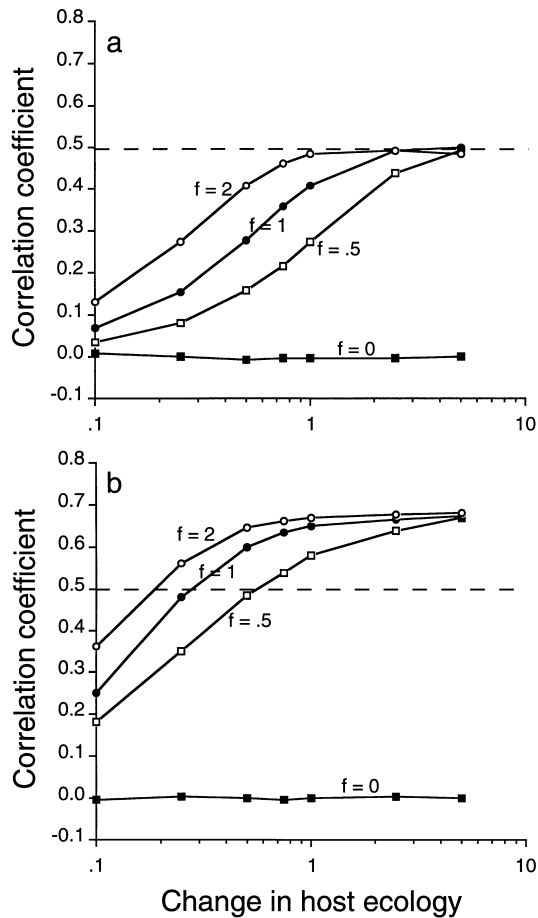
Fig. 4. Plot of the strength of the relationship between host ecology and parasite species richness, as a function of the standard deviation of changes in host ecology during host speciation events, or S.D., when $P = q = 0.1$ (a), and when $P = q = 0.3$ (b). The relationship between host ecology and parasite species richness was assessed with a correlation forced through the origin using phylogenetically independent contrasts. Results are presented separately for different values of f, the coefficient determining the strength of the effect of host ecology on $P*$ and $q*$. Each point is the average of correlation coefficients obtained from 10 000 separate simulations. The broken line represents the critical value ($\alpha = 0.05$) of the correlation coefficient for 15 contrasts (d.f. $= 14$).

blages. Here, we used computer simulations that trace the evolutionary history of one such ancestral assemblage through several host speciation events. We found that parasite extinction or colonisation must be frequent events, or strongly linked to host ecology, or both, in order for a relationship between

host ecology and parasite community richness to be detectable statistically. The simulations suggest that if acquisitions or losses of parasites are rare or only slightly influenced by host ecology, parasite communities will evolve in an almost entirely stochastic fashion as their host lineage branches out. We also found that divergence in host ecology between sister host lineages must not be trivial following a branching event for a relationship between host ecology and parasite species richness to emerge.

Using host species as independent statistical observations, several recent studies have reported relationships between some ecological trait of hosts and the richness of their parasite assemblages [6, 7, 25]. The results of the present simulations demonstrate clearly that simple cross-species correlations have inflated values and are likely to lead to invalid conclusions (see also Purvis et al. [23]). Repeating these analyses using correlations among independent contrasts can sometimes give similar results, e.g. compare Rohde et al. [7] with Poulin and Rohde [26], but often the conclusions reached will be widely different [11]. Because of the potentially important component of any parasite community that is inherited from an ancestral host, comparisons among host species should always control for phylogenetic effects. Our simulations show, however, that such tests have lower power to detect relationships between host ecology and parasite species richness. This is not a statistical artefact: with a fully resolved phylogeny like the one we used, a single degree of freedom is lost when using phylogenetic contrasts instead of host species values and the risk of type II error is therefore not greatly inflated. With real data, however, things are usually different: comparable data are typically available for a limited number of species whose phylogenetic relationships are poorly resolved. Most proper comparative analyses therefore have low power. Thus, significant correlations found using independent contrasts must be limited to cases where the effect of host ecology on parasite gain or loss is strong, and weaker effects go undetected by this conservative method.

We have made a number of simplifying assumptions in our model, and kept some parameters constant in the simulations, whereas in nature they may vary spatially and temporally. We did not allow the

size of the pool of parasite species to change during host evolution, or to vary between different branches of the phylogeny. Since hosts in the simulations could become saturated with parasite species (when richness equals the size of the parasite pool), the size of the pool determined maximum species richness, just as regional species richness may regulate local species richness in communities of free-living organisms [27]; but see [28]. However, simulations using an infinite parasite pool did not change our conclusions.

Interactions between parasite species may also affect how many parasite species can coexist in one host population or species [29]. By initially keeping the size of the pool of parasite species constant and ignoring interspecific interactions, we tried to emphasise the effects of the other parameters studied.

We also maintained the probabilities of parasite extinction and colonisation constant through time and among different regions of the host tree. The two probabilities were also varied independently (Figs 2–3), whereas in nature they may be coupled. For instance, colonisation rates may increase when extinction rates are high and several niches are vacated on local hosts [30]. In our models, high rates of both colonisation and extinction make ecological influences easy to detect. Clearly, if one or both these probabilities are not always relatively high during the simulated host evolution, the relationship between host ecology and parasite species richness will be more difficult to detect. Thus, our conclusion that such relationships can only appear under certain circumstances is based on an ideal scenario and is, therefore, likely to be conservative.

How common are losses and acquisition of parasite species during the evolution of a host lineage? This is a difficult question to answer, but some estimates may be obtained from studies of host–parasite cospeciation. There are two main approaches to the reconstruction of the history of hosts and their parasites. The first, parsimony analysis [31], may overestimate the frequency of host switches, or host colonisation events [17], and has been limited to studies of helminth parasites of vertebrates. The second method, reconciliation analysis [32], does not incorporate host switches as an explanation of observed associations, and may

overestimate the frequency of extinctions [17]. Studies using this method are still few, and have mostly been performed on vertebrates and their ecto-parasites, e.g. chewing lice on pocket gophers [33], and feather lice on seabirds [18]. Thus, the results of all these cospeciation studies may only provide estimates of maximum frequencies of extinction and colonisation. If we divide the number of postulated extinctions by the cumulative number of parasite species reaching each branching event in the host tree, we get maximum frequency values between 0.2 and 0.3. Note that a more recent version of reconciliation analysis [17], which incorporates host switching, leads to much reduced rates of extinction. Frequency of colonisation is more difficult to estimate because there is no information about the available pool of species at each branching event in the host phylogeny. There is some debate regarding the frequency of colonisation events [34, 35], but they are likely to be rare events. Therefore, actual probabilities of extinction and colonisation are likely to be relatively low compared with the highest values used in the simulations, which could make any influence of host ecology difficult to detect using correlations among independent contrasts.

What sort of parasite communities are likely to be influenced by the ecological characteristics of hosts? We have no detailed knowledge of extinction and colonisation rates in different groups of parasites and, therefore, can not make any solid predictions. However, broad differences in host specificity between different types of parasites can suggest differences in the frequency of host colonisation. Generally, parasites acquired by hosts through ingestion have a wider range of suitable host species than parasites transmitted by free-living stages and acquired through skin contact, or penetration, or both [36]. Colonisation of new hosts may, therefore, be more frequent among the former parasites than among the latter. Because acquisition of new parasites through ingestion is largely dependent on the frequency at which the host eats larval stages, host traits such as body size and diet should influence colonisation rates. Thus, we may expect a stronger effect of host ecology on the composition of gastrointestinal helminth communities than on that of ectoparasite communities. There is not

enough information available at present from studies in which phylogenetic influences were removed to assess this prediction.

Recent reviews have highlighted some of the problems associated with the identification of the key determinants of species richness in parasite communities [37]. Host phylogeny may be the most serious confounding variable masking the effect of ecological variables, but its influence has been mostly ignored to date. Phylogeny can affect not only species richness but also species composition of parasite communities. Kennedy and Bush [24] have identified two distinct elements making up parasite communities of salmonid fishes, i.e. a phylogenetic element consisting of salmonid–specialist parasite species, and an ecological element including other parasites acquired from other sympatric host species. The relative importance of the ecological element varies among populations and increases with the distance from the geographical origin of the host species. Thus, both inherited and acquired parasites make up parasite communities, but their presence is the product of distinct phenomena. No doubt host ecology can influence the likelihood of acquiring new parasite species or losing ancestral ones. There is sufficient correlational and experimental evidence from studies of parasite acquisition by conspecific host individuals in a population to show that factors such as body size can explain the variability in numbers of parasite individuals or parasite species (e.g. in fishes, [38, 39]). However, demonstrating the influence of host ecology over evolutionary time by examining patterns in parasite community richness across extant host species is likely to be less straightforward. As shown here, available estimates of parasite extinction and colonisation rates suggest that no matter how strongly these events are linked with changes in host ecology, they may simply be too rare to generate detectable relationships between host ecology and parasite community richness.

Acknowledgements

We are grateful to J. Moore, A. Paterson, and K. Rohde for valuable suggestions on earlier drafts.

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