PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2011) **366**, 2379–2390
doi:10.1098/rstb.2011.0048

Review

The comparative ecology and biogeography of parasites

Robert Poulin[1,*], Boris R. Krasnov[2], David Mouillot[3] and David W. Thieltges[4]

[1] *Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*
[2] *Mitrani Department of Desert Ecology, Institute for Dryland Environmental Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel*
[3] *UMR CNRS-UM2-IFREMER-IRD 5119 Ecosystemes Lagunaires, University of Montpellier 2, CC093, FR-34095, Montpellier Cedex 5, France*
[4] *Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*

Comparative ecology uses interspecific relationships among traits, while accounting for the phylogenetic non-independence of species, to uncover general evolutionary processes. Applied to biogeographic questions, it can be a powerful tool to explain the spatial distribution of organisms. Here, we review how comparative methods can elucidate biogeographic patterns and processes, using analyses of distributional data on parasites (fleas and helminths) as case studies. Methods exist to detect phylogenetic signals, i.e. the degree of phylogenetic dependence of a given character, and either to control for these signals in statistical analyses of interspecific data, or to measure their contribution to variance. Parasite–host interactions present a special case, as a given trait may be a parasite trait, a host trait or a property of the coevolved association rather than of one participant only. For some analyses, it is therefore necessary to correct simultaneously for both parasite phylogeny and host phylogeny, or to evaluate which has the greatest influence on trait expression. Using comparative approaches, we show that two fundamental properties of parasites, their niche breadth, i.e. host specificity, and the nature of their life cycle, can explain interspecific and latitudinal variation in the sizes of their geographical ranges, or rates of distance decay in the similarity of parasite communities. These findings illustrate the ways in which phylogenetically based comparative methods can contribute to biogeographic research.

Keywords: distance decay of similarity; host specificity; geographical range; latitude; life cycles; phylogenetic signal

1. INTRODUCTION

Comparisons between different species, whether expressed as casual observations or based on quantitative analyses, have been a powerful heuristic tool in the development of ecological thought [1,2]. For example, several classical studies of resource use and species coexistence have relied heavily on differences among closely related species to generate hypotheses or test their predictions [3–5]. In addition, much coarser comparisons can be made by any amateur biologist. For instance, elephants and tortoises live for decades, whereas mice and frogs live for a few years at best, an obvious pattern hinting at a link between body size and longevity. It could be argued that comparative ecology uses a bottom-up approach, starting with comparisons among a subset of species to derive more general principles and establish the generality of evolutionary phenomena.

In contrast to the bottom-up approach employed by comparative ecology, biogeographic studies tend to take a top-down approach. Biogeography aims to document and understand patterns of biodiversity at large spatial and temporal scales [6]. It relies heavily on geological processes and historical events to explain the distribution of specific organisms. At the intersection between comparative ecology and biogeography, macroecology has emerged based on a large body of theory linking individual-level traits with statistical patterns of abundance, distribution and diversity, with its scope now spanning all levels of organization from genes to ecosystems [7–10]. Though the interests of both disciplines overlap, macroecology distinguishes itself from biogeography by its focus on the relationships between organisms and their environment as seen through these statistical patterns [11,12]. Macroecology is sometimes criticized for making limited use of geographical data and focusing too

---

[*] Author for correspondence (robert.poulin@otago.ac.nz).

One contribution of 10 to a Theme Issue 'Biogeography and ecology: two views of one world'.

much on statistical relationships among species traits [13]. However, mapping species distributions alone cannot distinguish among competing hypotheses proposed to explain large-scale patterns, whereas statistical analysis of interspecific ecological data can [14]. Thus, comparisons among species represent one of the most fundamental tools of macroecology, and via this shared perspective, comparative ecology can inform biogeographic research.

Comparative ecology, like everything else, only makes sense in the light of evolution. The traits shared by conspecific individuals are the product of evolution, as are the differences that exist between species. Comparisons made between species must therefore be placed within the context of their evolutionary history, as the degree of independence between any two species, in a statistical sense, is proportional to their phylogenetic affinities [15]. There has been much debate among ecologists regarding the need to control for phylogenetic influences in comparative analyses, or the benefits of doing so [16–18]. For instance, is a phylogenetic correction necessary when relating variation among species to the operation of immediate environmental factors acting on ecological rather than evolutionary time-scales? [19] Mounting evidence suggests, however, that numerous ecological and life-history traits show a strong phylogenetic signal, i.e. they vary among species in direct proportion to their shared phylogenetic history [20]. The phylogenetic non-independence of ecological traits extends to properties such as niche breadth and geographical range size ([21–24], but see [25]), though such properties are often assumed by ecologists to be strong reflections of environmental influences and only indirect phenotypic expressions of genotypes. Early macroecological studies based on comparisons among species generally did not include a phylogenetic correction. However, given the accumulating evidence of its ubiquitous importance, and the availability of phylogenetic information for a rapidly increasing range of taxa, the trend has changed; for most research questions, it is now recommended practice to consider the relationship between evolutionary history and current macroecological patterns [26].

The goal of this review is to illustrate how comparative ecology incorporating phylogenetic information can shed light on biogeographic patterns and their link to ecological traits. We will achieve this by using our own studies on parasitic organisms to illustrate both the basic approach and some key findings. Our case studies will be limited to two types of parasites: fleas and helminths. Fleas (Siphonaptera) are characteristic ectoparasites of mammals and are most abundant and diverse on small- and medium-sized host species. They usually alternate between periods when they feed on the body of their host and periods when they occur in its burrow or nest. In most flea species, egg, larval and pupal development is entirely off-host. The larvae are usually not parasitic and feed on debris and materials found in the burrow and/or nest of the host. In contrast, parasitic worms or helminths (Trematoda, Cestoda, Nematoda, Acanthocephala) are internal parasites characterized, except for some nematode taxa, by a complex life cycle requiring the sequential infection of two or more hosts of different species for the completion of a single parasite generation. Adult worms live inside a vertebrate definitive host, whereas their larval stages infect either vertebrate or invertebrate intermediate hosts, depending on the parasite species; transmission among these hosts occurs either via predation of one host by the next one in the life cycle, or through free-living infective stages. Thus, a review of flea and helminth comparative ecology incorporates two broad and distinct sets of life history and host-exploitation strategies.

Our review begins in §2 with a look at the close links between parasite and host distributions, and at how phylogenetic history has shaped the traits of extant parasite taxa. In §3 we briefly discuss the various ways in which phylogenetic data can either inform or confound comparative analyses in parasite ecology and biogeography. We follow this in §4 by focusing on two fundamental properties of parasites, their niche breadth (=host specificity) and the nature of their life cycle, and illustrate how they can shape biogeographic patterns. Indeed, we show that these two individual-level properties can be used to generate testable hypotheses about interspecific variation in parasite distributions. §6 counters this by demonstrating how a key host trait, i.e. vagility or dispersal ability, can in turn drive biogeographic patterns in parasite assemblages. Finally, in §7 we identify gaps in our understanding of parasite biogeography, and highlight the ways in which a comparative approach can fill them in.

2. FUNDAMENTALS OF PARASITE ECOLOGY

Parasites present some interesting challenges for comparative studies in ecology and biogeography. By definition, parasites are dependent upon their host for essential resources. This does not simply involve the acquisition of nutrients, but also entails physical attachment to the host or residence within the latter's body for prolonged periods of time, if not for most of the parasite's life. This has important implications for the spatial ecology and evolutionary history of parasites.

Firstly, the spatial distribution of parasites must necessarily be closely coupled with that of their hosts. Because parasites require suitable hosts for nutrients and other resources, they cannot occur where those hosts are absent. Therefore, the maximum geographical range of a parasite must equal the combined ranges of its hosts. As a corollary, because parasites are where the hosts are, parasite species richness must covary across localities with host species richness [27–29]. Assuming that most host species harbour at least one host-specific parasite species, then all else being equal, a positive relationship between host and parasite species richness is inevitable and generally supported, independent of variability among areas in either their size or how well they have been investigated for parasite diversity (figure 1). Hotspots of host diversity are thus generally hotspots of parasite diversity, too.

Secondly, the tight dependence of parasites on their hosts leaves a deep imprint on many parasite ecological

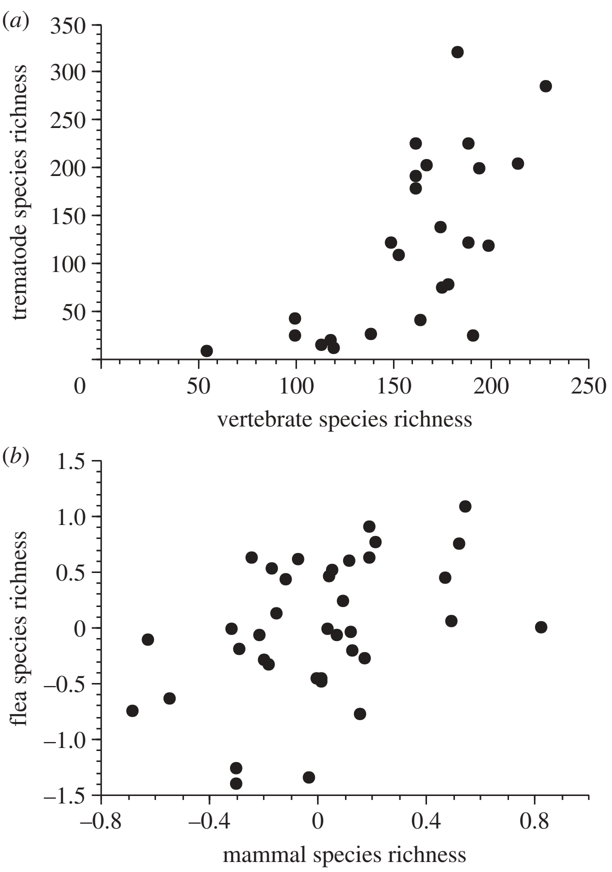

Figure 1. Parasite species richness as a function of host species richness across geographical areas, for (*a*) freshwater trematodes and their vertebrate hosts from 25 biogeographic regions in Europe, and (*b*) fleas and their small mammalian hosts from 37 regions of the world. Data on fleas and mammals are corrected for host sampling effort and area size, i.e. they are residuals from a multiple regression (data from Krasnov *et al.* [28] and Thieltges *et al.* [29]).

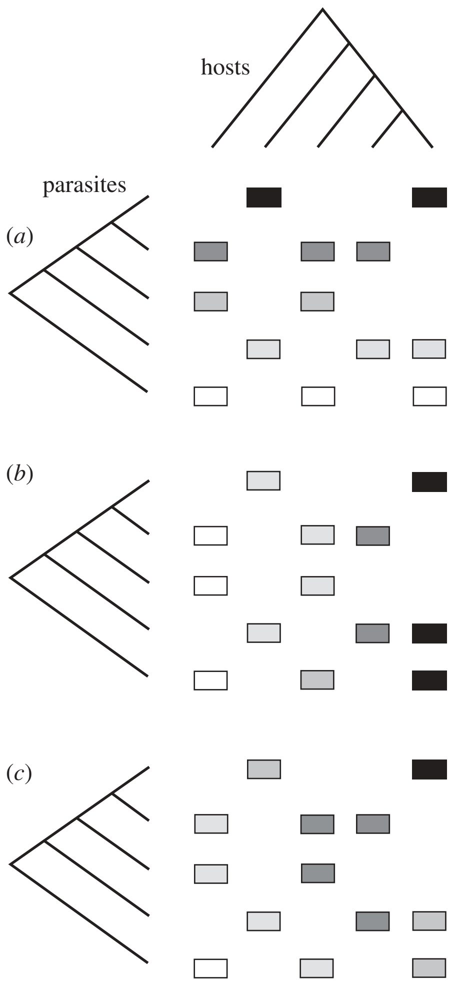

Figure 2. Hypothetical scenarios for the influence of host or parasite phylogeny on trait expression in five parasite species occurring on five host species. Realized host–parasite species combinations are indicated by boxes aligned with branch tips of either the host or parasite phylogenetic tree; the parasites are assumed to be generalists capable of infecting more than one host species, and in turn each host species harbours more than one parasite species. The magnitude of trait expression is indicated by the shading inside each box, ranging from low (white) through moderate (grey) to strong (black) expression. Trait expression can be influenced (*a*) by parasite phylogeny only, regardless of what host species a parasite infects, (*b*) by host phylogeny only, to a similar extent in all parasites infecting a given host species or (*c*) by a combination of both phylogenies acting in concert.

properties. However, host characteristics have varying degrees of influence on parasite biology, depending on which trait is considered: parasite traits mapped onto a host phylogeny may thus show varying degrees of fit (figure 2). Some properties of parasites are true parasite species traits, independent of the host. For example, allocation of reproductive investment between testis size and testis number varies among cestode species within a clade, but independently of the host species they exploit [30]. Other parasite species traits show a strong phylogenetic signal but are additionally modulated by the identity or characteristics of the host. For example, interspecific variation in parasite body size is often related significantly to variation in host body size, especially for internal parasites [31–33]. Other traits are even more strongly influenced by the host: they are best considered as coevolved properties of a host–parasite association rather than specific traits of either antagonist. For instance, parasite virulence, i.e. the harm caused to the host by infection and usually measured as parasite-induced reduction in host fitness, can hardly be seen purely as a parasite trait [34]. Instead, it is the outcome of a genetically determined parasite strategy of resource exploitation, and of host counter-adaptations including immunological responses and/or compensatory mechanisms. Indeed, the same parasite species can cause very different fitness losses in different but closely related host species [35,36].

In addition, some other variables, like parasite species richness in different host species, are arguably true host traits (figure 3). Through the phylogenetic history of host species within a given clade, parasite species are acquired or lost like other traits, and they can be mapped onto a host phylogeny [37]. Parasite species are either inherited from an ancestor (by cospeciation), gained (via host-switching or colonization, or by intra-host speciation) or lost (after missing the boat during speciation, or following extinction). These changes in numbers of parasite species occur at different rates in different host lineages, possibly influenced by host ecological traits, making

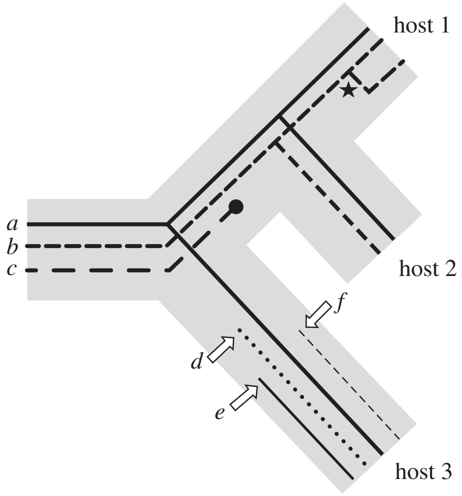

Figure 3. Changes in parasite species richness in host lineages over phylogenetic time. The shaded area represents the phylogenetic relationships among three host species. The lines mapped onto this phylogeny identify parasite lineages (denoted *a*–*f*). When the host speciates, parasites often co-speciate such that each daughter host species inherits the ancestor's parasites (lineage *a*). Parasites can also 'miss the boat' during host speciation (lineages *b* and *c* not inherited by host 3), or go extinct some time after host speciation (lineage *c*, black circle), and thus be absent from one or more daughter host species. New parasites are acquired by hosts through colonization (i.e. host-switching, lineages *d*–*f*, shown by arrows) or following intrahost parasite speciation, i.e. parasite duplication without host speciation (in lineage *b*, shown by star). The result is that related host species harbour different numbers of parasites from each other and from their common ancestor.

it essential to control for host phylogeny in any test of the determinants of parasite species richness [38]. Thus, the extent to which host and/or parasite phylogenetic influences may affect the expression of a trait is highly variable. Depending on the nature of the variables included in a comparative study, one may therefore need to take into account parasite phylogeny, host phylogeny or both.

3. MEASURING PHYLOGENETIC INFLUENCES ON PARASITE ECOLOGY

(a) *Phylogenetic signal*

With respect to morphology, closely related species tend to share attributes inherited from their common ancestor. However, with respect to ecological attributes, phylogenetic niche conservatism is best seen as an evolutionary conjecture, which stipulates that closely related species should be more ecologically similar than expected based on the timing of their phylogenetic divergence [22,39]. As a hypothesis, it is usually tested by measuring a statistical pattern known as the phylogenetic signal, which corresponds to the degree of phylogenetic dependence of a given character [40]; a null phylogenetic signal simply indicates that the character is totally independent from the phylogeny. As a trait experiencing random evolution (Brownian motion) will inevitably result in at least a weak phylogenetic signal, phylogenetic niche conservatism should lead to a stronger phylogenetic signal than expected under Brownian motion. Hence, phylogenetic niche conservatism can also be defined as the tendency for related species to exhibit greater phylogenetic signal than expected under a scenario of Brownian trait evolution. Establishing the presence of a phylogenetic signal among comparative data is the first step in a comparative analysis, as it determines whether correcting for phylogenetic influences is necessary.

Several methods have been proposed for the detection of phylogenetic signals, all using a slightly different approach to compare the distribution of trait values among the branch tips in a phylogenetic tree to that expected from some null model [39–43]. Each method has its own merits and disadvantages. For instance, they are not equally robust to incomplete phylogenetic data on branch length or topology, and they make different assumptions about underlying models of character change [43]. Nevertheless, when applied to the same data, different methods generally reveal similar patterns of phylogenetic resemblances among the traits of species within a clade [44]. Applying any of these methods to several comparative datasets typically reveals ubiquitous phylogenetic signals, not just for morphological traits but also among ecological and behavioural traits [20,40,45].

Several traits of parasites also show conservatism based on phylogenetic relationships. Sometimes, no formal test is necessary to demonstrate this pattern. For instance, the complex life cycles of related trematodes typically display similar patterns with respect to the types of host used. Species in the family Schistosomatidae all have a two-host life cycle involving a snail and an endothermic vertebrate, whereas those in the family Opecoelidae have a three-host cycle involving a snail, another invertebrate (usually a crustacean) and a fish. The same sort of conservatism can be seen among families of nematodes or cestodes, indicating a strong phylogenetic signal in ontological niche shifts by parasites, corresponding to transmission from one host to the next during their development. Other aspects of parasite biology are more labile and not so obviously subject to phylogenetic signals. For instance, the number and specific identities of host species exploited by a parasite species at any given stage of its life cycle vary among closely related species. Nevertheless, when tested rigorously, sister species of helminth parasites of birds, and of fleas parasitic on small mammals, are more similar than expected by chance for numbers of host species used or their taxonomic diversity, suggesting a phylogenetic signal [46]. Local availability of host species can influence estimates of how many hosts are used, or of which host species are preferred. Indeed, generalist flea species exploit subsets of host species only slightly taxonomically distinct from random subsets taken from the local species pool, suggesting strong local constraints affecting measures of host use [47]. This probably explains why the phylogenetic signal in the number of host species used by given flea species, as well as in the average abundance achieved by fleas on their hosts, is much stronger when based on continental-scale data than on regional-scale data [44]. Thus, when examined at the appropriate scale, ecological traits of parasites generally show clear phylogenetic signals.

(**b**) *Correcting for phylogenetic influences*

When a phylogenetic signal has been demonstrated (or when one is strongly suspected) in a comparative dataset, correcting for phylogenetic influences while testing for associations among ecological variables is necessary, or at least well justified. The phylogenetically independent contrast, or PIC, method has been the main way of achieving this over the past 20 years [48]. Put simply, the method computes the difference in trait values between sister branches issued from the same node in a phylogeny, and uses these differences, or contrasts, in statistical analyses instead of the species values on the branch tips [15,48,49]. In the past decade, the phylogenetically corrected generalized least squares (GLS) method has rivalled the PIC method in popularity [20,50–52]. Contrary to the PIC method, GLS tests for the relationships between original character values rather than between contrasts. This method controls for the confounding effect of phylogeny by incorporating the phylogenetic autocorrelation of the data in the error structure [20,50]. In essence, GLS employs maximum-likelihood estimation of an index of phylogenetic dependence and incorporates it into the analysis to control for any phylogenetic effect [52]. The index of phylogenetic dependence is essentially a measure of phylogenetic signal [51]. Both PIC and GLS are actually similar in assuming a Brownian model of trait evolution to model the expected covariance of traits among species [53]. Most applications of PIC and GLS involve dependent variables that are continuously distributed, but analysis of binary dependent variables within a phylogenetic context is also possible using a logistic regression approach [54]. All these and other related methods, like the recently proposed phylogenetic principal component analysis [55], can be implemented with a range of readily available statistical packages.

The relevance of adopting these methods instead of performing analyses on ‘raw’ trait values becomes clear when their performance under a range of scenarios is compared with that of a straight correlation across species values [56]. Based on analyses of simulated data, PIC, GLS and other comparative methods incorporating phylogenetic information are generally better in detecting existing relationships among traits than correlations among species values regardless of the evolutionary model used to generate the data. The outcome of analyses of real biogeographic data also often depends on whether or not phylogenetic information is considered. For instance, Krasnov *et al.* [57] tested for an interspecific relationship between the latitudinal centre of the geographical range of fleas parasitic on small mammals and their host specificity, the latter measured as the average taxonomic distinctness among the host species used by a flea (see §4*b*). When the raw species values were analysed, host specificity did not correlate with the position of the centre of the geographical range ($p = 0.3$). However, correcting for the confounding effect of phylogeny using PIC revealed a significant positive correlation between these two parameters ($p < 0.01$). The contrasting results suggest that phylogenetic effects may mask true relationships. The adaptive component of the geographical pattern resulting from species-level responses occurred independently of phylogeny, but could only be seen after the strong phylogenetic signal was neutralized.

(**c**) *Estimating relative effects of phylogeny and other factors*

Correcting for phylogenetic influences may serve some purposes, such as allowing the ‘phylogeny-free’ analysis of comparative data. In other cases, phylogeny might be of interest in its own right, e.g. one might want to estimate the relative effects of phylogenetic conservatism versus other factors on the expression of particular species traits. Two related methods, the phylogenetic eigenvector regression (PER) and multiple regression on distance matrices (MRM), provide ways of achieving this [58–60]. In these multivariate analyses, all predictor variables and the response variable are expressed as distance matrices, all of which are unfolded into distance vectors. In simple terms, a matrix of pairwise phylogenetic distances is constructed for all species being compared; these may consist of patristic distances, i.e. the sums of branch lengths linking two species in a tree. This phylogenetic distance matrix is then used as a predictor variable; other predictor variables and the response variables may include geographical distances between the geographical ranges of species as well as interspecific differences in a range of traits. The significance of the regression model as well as the effects of individual predictors are determined using permutations, and the fraction of the variation explained by each predictor can also be calculated. These approaches are already used to address biogeographic questions [60,61].

In parasite biogeography, this sort of method can be very useful when the nature of a trait requires correcting simultaneously for both parasite phylogeny and host phylogeny, or when one must evaluate which of the two phylogenies has the greatest influence on trait expression. This situation would not arise if the coevolutionary history of a clade of parasites with their particular clade of hosts followed Farenholz’s rule, an old hypothesis in parasitology stating that the phylogenetic tree of parasites is a mirror image of that of their hosts. Some of the earliest studies of host–parasite coevolutionary history using molecular phylogenetics indeed suggested almost perfect congruence between host and parasite phylogenies (e.g. [62]). In such cases, controlling for parasite phylogeny in a comparative analysis would automatically also control for host phylogeny without any additional steps. However, subsequent co-phylogenetic studies have indicated that parasite trees that mirror host trees are exceptions rather than the norm; indeed, frequent host-switching and less-than-strict host specificity seem to characterize many host–parasite associations (see [63] for review). If both the evolutionary history of parasites and that of their hosts are believed to influence the trait under study, then simultaneous correction for both sets of phylogenetic influences is required. While the original methods developed for comparative analysis, like PIC, allow control for only one phylogenetic tree, methods such as PER and

MRM can deal with multiple phylogenies. All host–parasite species combinations just need to be mapped onto the branch tips of both a host phylogeny and a parasite phylogeny before each phylogeny gets converted into a distance matrix [64].

Comparative ecology now comes with a comprehensive set of tools to investigate relationships among species traits, including those relating to geographical distribution, while accounting for the evolutionary baggage carried by all extant species via inheritance from common ancestors. The following sections will apply these tools to varying degrees in an attempt to extract 'phylogeny-free' patterns reflecting the true influence of ecological properties on biogeographic phenomena. More specifically, we will focus on key ecological properties of parasites or their hosts, make predictions regarding their likely effects on the geographical distributions of parasites, and test those predictions using methods that eliminate as much as possible any confounding influence of phylogenetic history.

4. PARASITE NICHE BREADTH AND BIOGEOGRAPHY

The host provides both food and shelter for parasites, and therefore the simplest way of measuring realized niche breadth for parasites is to equate it with host specificity. Different measures of host specificity exist, and hereafter we will consider two of them: the number of host species used by a parasite, and their phylogenetic diversity, which can be measured as the average pairwise taxonomic or phylogenetic distance between the host species used [65]. As discussed in §3*a*, host specificity is also phylogenetically conserved, with closely related parasite species showing more similar values of host specificity than expected by chance [44,46]. Finally, host specificity is a key property of parasites: it is a determinant of their local extinction risk and of their likelihood of successful establishment following introduction to a new region, with generalist species less prone to local extinction and better invaders than specialists [66,67]. In addition, in the case of fleas, generalist species also achieve higher abundance on their hosts, i.e. greater numbers of individuals per individual host [68]; therefore, host specificity is also a determinant of individual fitness and population success. For these reasons, we might expect host specificity to explain some of the interspecific variation in the geographical distribution of parasites.

(a) *Niche breadth and geographical range size*

Interspecific relationships between the degree of specialization for resources and the size of the geographical range have been reported for various taxa [8,69]. The niche breadth hypothesis provides a simple explanation [70]: specialists can tolerate only limited abiotic conditions or feed on a restricted range of resources, and therefore can only exist in a narrow subset of localities, whereas generalists with broad tolerance and diets can exist in a wider range of places. For parasites, this should mean that generalist species (with low host specificity) have a wider geographical range than specialists. A larger geographical range in generalist parasites may result, in part, from the larger total range size of their entire host species combined. In addition, the probability that a parasite can persist in any locality should depend on its ability to exploit local hosts, regardless of the latter's geographical distribution. Generalist parasites are more likely than specialists to cope with host extinctions and changes in host abundances at these local scales, allowing them to maintain larger geographical distributions. Thus, the niche breadth hypothesis is a viable explanation for any link between host specificity and geographical range size in parasites.

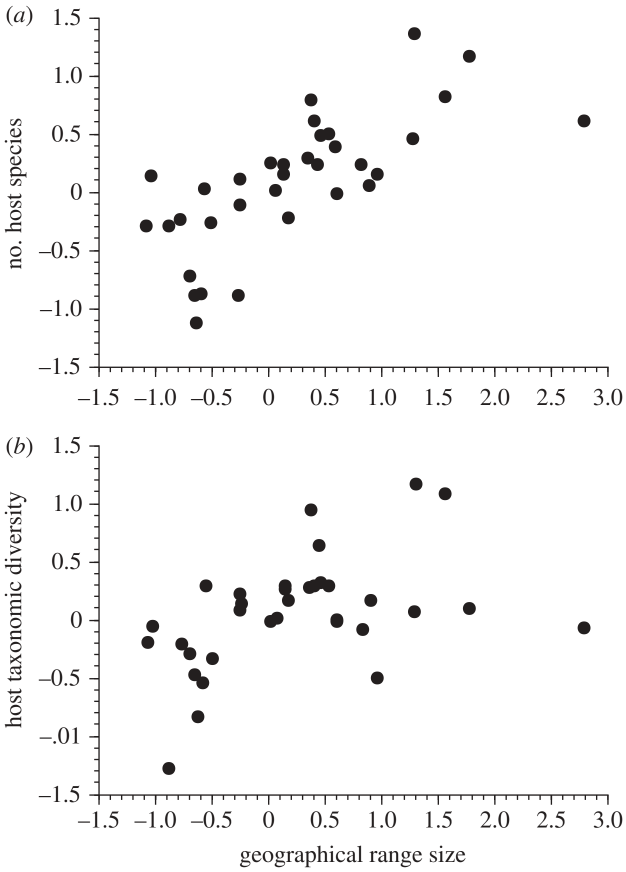

Figure 4. Relationships between geographical range size (square kilometres) and two measures of host specificity, (*a*) the number of host species exploited and (*b*) their average taxonomic distinctness, across flea species parasitic on small mammals in Australia. Data are phylogenetically independent contrasts computed on log-transformed values (data from Krasnov *et al.* [71]).

This was tested for fleas parasitic on small mammals, using data for a total of 341 flea species from seven distinct geographical regions and employing the PIC method [71]. In all regions, generalist flea species achieved a larger geographical range than specialist species confined to a narrow spectrum of host species (figure 4). This was true if host specificity was measured as the number of host species used by a flea or as their taxonomic diversity. The independence of this result from any phylogenetic inheritance strengthens the causal inference one can make between parasite niche breadth and geographical range size, and also suggests that the underlying mechanism is not specific to the particular flea taxa included in the study. However, it remains unclear whether this pattern holds true for other parasite and host groups, and future studies will need to revisit the relationship between parasite niche breadth and range size.

(**b**) *Latitudinal gradients in parasite niche breadth*

Latitudinal gradients in numbers of species or in their properties represent some of the best-documented large-scale patterns in biogeography. The interrelationships among latitude, geographical range size and niche breadth are particularly informative, as they may represent the visible outcome of universal ecological processes [72–75]. One such gradient, known as Rapoport's rule, involves the widely reported increase in the geographical range size of species with increasing latitude, i.e. species at high latitudes tend to have broader geographical ranges than those at lower latitudes [72,75]. Another latitudinal gradient with good empirical support, at least for some taxa, is the positive relationship between latitude and niche breadth, with generalist species occurring at greater frequency at high latitudes and specialists being more common in the tropics [74]. The mechanisms linking these two broad patterns have been hypothesized to involve the effect of high species richness on specialization as (i) species richness generally peaks at low latitudes, (ii) specialist species with narrow niche breadth are more frequent in species-rich communities, and (iii) as seen above, generalist species achieve larger geographical ranges than specialists [74]. To date, however, empirical tests of these patterns have mostly been performed without corrections for phylogenetic relatedness, and whether they exist as the outcome of ecological processes or following evolutionary inheritance remains unclear.

Using data on 120 flea species parasitic on small mammals in the Palaearctic, and employing the PIC method, we confirmed that both geographical range size and niche breadth, measured as the taxonomic diversity of host species used, increase with increasing latitude [57]. These patterns are independent of phylogenetic influences (figure 5) and, in the case of host taxonomic diversity, became apparent only after correcting for those influences. However, the real challenge will be determining to what extent they are the outcome of processes acting on parasites as opposed to being a consequence of parasite biogeography merely mirroring host biogeography. Indeed, mammals serving as hosts for fleas also show latitudinal gradients in niche breadth and geographical range size (e.g. [76,77]). Testing whether these patterns develop independently among their parasites as opposed to being constrained to follow host patterns may require a simultaneous correction for parasite phylogeny, host phylogeny and host ecology, using one of the methods mentioned earlier.

5. PARASITE LIFE CYCLE AND BIOGEOGRAPHIC PATTERNS

Host specificity is not the only key parasite property that may shape parasite biogeography. Except for a few nematode taxa, helminth parasites have complex life cycles requiring a parasite to infect two or more host species, in a given order, in order to complete a single generation. The parasite completes a new developmental stage inside each host, and shows different levels of host specificity at each stage. The life cycle can thus add another layer of complexity to the host requirements of parasites, making it also a key determinant of their risk of local extinction and of their likelihood of surviving following introduction to a new region [66,67]. General life cycle patterns are also clearly phylogenetically conserved, i.e. members of any given genus or family must use hosts belonging to the same broad taxon to complete their life cycle. For example, trematode species of the family Cryptogonimidae almost invariably have a snail to small-fish to large-fish life cycle, whereas those of the family Strigeidae tend to have a snail–fish–bird cycle.

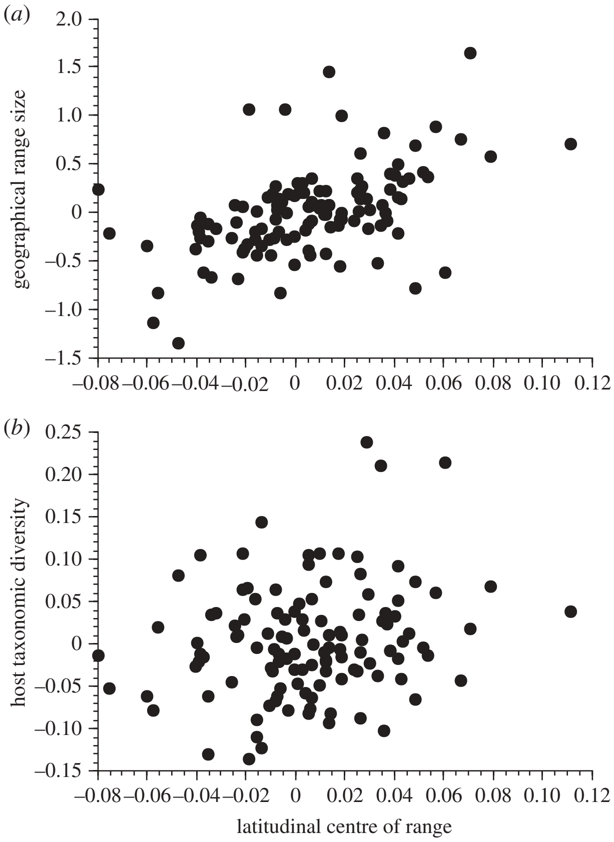

Figure 5. Relationships between the latitude of the centre of the geographical range and (*a*) flea geographical range size (square kilometres) and (*b*) the average taxonomic distinctness of host species exploited, across flea species parasitic on small mammals in the Palaearctic. Data are phylogenetically independent contrasts computed on log-transformed values (data from Krasnov *et al.* [57]).

The variation among the types of hosts used by parasites suggests a mechanism through which the life cycle can influence biogeographic variables. Parasites rely almost entirely on their hosts, in particular the definitive host in the case of helminths, for dispersal at both small to large spatial scales. Therefore, the vagility of the definitive host should be the main determinant of a parasite's dispersal potential [78]. For instance, all else being equal, when comparing helminth parasites that spend the first part of their life

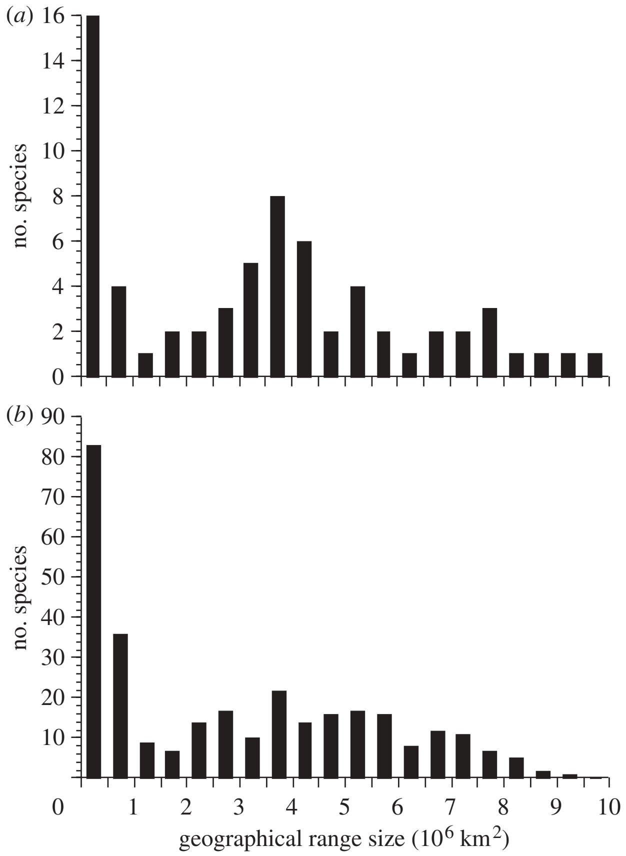

Figure 6. Frequency distribution of geographical range sizes for European freshwater trematode species parasitic in (*a*) fish definitive hosts ($n = 67$) and (*b*) bird definitive hosts ($n = 307$) (data from Thieltges *et al.* [80]).

cycle in freshwater habitats, we would expect those using birds or mammals as definitive hosts to disperse more readily across the region than those using fish, as the latter remain more or less confined to a single water body. This expectation is confirmed by phylogeographic studies on regional scales that find greater gene flow among lake populations of trematode species maturing in birds than among those maturing in fish [79]. We might also expect that host vagility is an important factor affecting geographical range size, as parasites of vagile hosts have a higher probability of dispersing to new localities than those exploiting hosts with limited vagility.

This prediction was tested with comparative data on European freshwater trematode species. In the absence of a comprehensive phylogeny of trematodes extending beyond the family level, the taxonomic affiliations (genus, family, etc.) of each species were entered as factors in a semi-nested design, in an attempt to distinguish between phylogenetic influences leading to conserved values and true effects of host vagility [80]. In the end, phylogenetic influences proved insignificant. The results of the analysis also showed that host vagility is not related to the size of trematode geographical ranges. In other words, parasites exploiting highly vagile definitive hosts such as birds do not achieve consistently larger geographical ranges than those using fish hosts that are thus restricted in their movements to a single lake or watershed (figure 6). Host dispersal may not be as important at continental scales as on the regional scales mentioned above, especially if other factors are at play. For instance, a general difference in host specificity between bird parasites and fish parasites, through its connection with range size, could offset any effect of host-dispersal abilities. These relationships should be revisited when good comparative data on the host specificity of European freshwater trematodes are compiled.

6. HOST DISPERSAL AND DISTANCE DECAY OF SIMILARITY

Although host vagility does not appear to influence the geographical range size of helminth parasites, it may nevertheless have important biogeographic implications. Host dispersal should facilitate the homogenization of parasite communities across geographical space. Like other assemblages, parasite communities in any given host species show a clear decay in compositional similarity as a function of the distance separating them: nearby host populations tend to have many parasite species in common, whereas distant ones share very few. This phenomenon applies to varying degrees to a wide range of host and parasite taxa [81–86]. Several mechanisms can act, alone or in combination, to produce a decrease of the similarity in species composition between two communities with increasing distance between them [87]. For instance, the spatial autocorrelation of climatic and abiotic variables can lead to species-sorting in geographical space, or landscape topography may constrain either direct or host-mediated dispersal of parasite species.

The rate at which similarity in parasite communities decays with increasing distance between host populations can be measured in many ways. These include the slope of the similarity-versus-distance relationship in log–log or semi-log space, or the halving distance, i.e. the distance at which similarity is reduced by half its maximum value as calculated from a linear regression [87]. All else being equal, we might expect similarity in parasite communities to decay at a slower rate among populations of a highly vagile host species, such as a bird, than among those of hosts with limited movement, such as freshwater fish constrained to physically separated water bodies. Such a pattern was observed in parasite communities of the marine snail *Hydrobia ulvae*, which serves as the first intermediate host for a range of trematode parasites that use either birds or fish as definitive hosts. The halving distance for the trematode species using birds as definitive hosts was approximately two to three times larger than for species using fish hosts, suggesting that host-dispersal ability is a strong driver of distance decay patterns [85]. However, tests of this prediction are challenging for several reasons. First, environmental differences between two localities can affect the similarity in their parasite communities independently of geographical distance [88,89]. Indeed, for a given geographical distance between two host populations, they are more likely to share parasite species if they occupy habitats with similar environmental conditions (figure 7). Second, geographical variation in the composition of parasite communities has only been

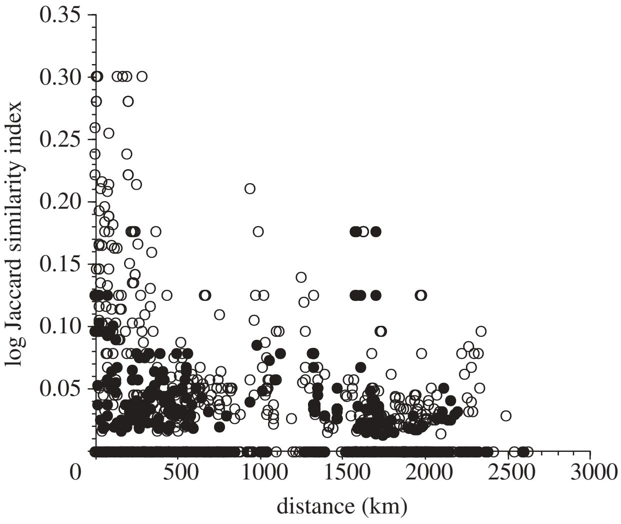

Figure 7. Similarity between parasite communities plotted against the geographical distance between them, for all pairwise comparisons of metazoan parasite communities found in three-spine stickleback, *Gasterosteus aculeatus*, populations from different localities in Eurasia. Similarity is measured as the Jaccard index, i.e. the proportion of shared parasite species out of the total from two localities. Different symbols show values for pairs of localities from the same habitat type based on salinity (both localities either marine or freshwater; open circles), or from contrasting habitats (one is freshwater and the other is marine; filled circles) (data from Poulin *et al.* [89]).

examined quantitatively in a handful of host taxa, which limits any inference about the role of their ecological characteristics [90]. Dispersal ability is not the only trait that varies among host species, and interspecific comparisons of the rates of distance decay in parasite community overlap among different host species will need to be performed within a phylogenetic framework, to account for other inherited similarities and differences. Two of the most fundamental questions in parasite biogeography, i.e. what determines variation in parasite diversity among host species and among areas, and what controls parasite species turnover in space, can only be properly answered if informed by phylogeny. While the former question has been addressed within a rigorous phylogenetic context (see [38,67,91]), the latter has not. Estimating rates of distance decay in similarity provide a quantitative measure of spatial species turnover in parasite communities, which now needs to be examined with proper comparative methods.

7. CONCLUDING REMARKS

The comparative approach has always been and will remain an essential tool for ecology and biogeography. It provides a solid conceptual and methodological bridge between the local-scale focus of ecology and the large-scale view of biogeography, by linking local selective forces with interspecific patterns of variation across space. Comparative ecology has had to overcome a few obstacles, some of which still stand. The main ones have been the reluctance of many ecologists to acknowledge the signature of phylogeny in studies of ecological phenomena acting on short time-scales, and the lack of robust phylogenies for a wide range of taxa. Nevertheless, the use of phylogenetically grounded comparative analyses has become standard, although there are still important challenges to be met. One of them is the need to incorporate both phylogenetic and spatial data into interspecific comparisons. The use of approaches based on distance matrices is an obvious way of achieving this (see [92]). A second important challenge for phylogenetically based comparative methods will be shifting the emphasis from p-values to effect sizes, and to allow for model uncertainty within an information theoretic framework (see [53]).

Comparative analyses assessing interspecific relationships among traits grounded in a phylogenetic framework have identified global patterns in parasite biogeography, and helped to distinguish among the possible underlying processes. In many cases, individual-level properties such as niche breadth (i.e. host specificity) or life-cycle characteristics are driving some emergent large-scale patterns in the distribution of parasites. Our understanding of the geographical determinants of parasite diversity remains patchy, however. A major problem is the availability of good data, as data on parasite diversity in any given area generally lag several years behind data on free-living organisms. As the examples above show, fleas parasitic on small mammals and trematodes of freshwater vertebrates rank among the better-studied host–parasite systems, simply owing to the availability of data compilations. However, it remains unclear how well the observed patterns hold for other parasite–host systems. There is a myriad of parasitological data buried in the literature, not only in Western journals but in particular in Russian and Chinese sources. As electronic databases are constantly growing, the compilation of extensive parasitological datasets should become increasingly feasible in the near future. At the same time, the availability of modern phylogenies for both parasite and host groups is also constantly growing, paving the way for comparative ecological studies of the effects of individual-level traits on large-scale biogeographic patterns.

As data become available, making sense of them will be a considerable challenge too, given that the ultimate drivers of parasite diversity are entangled among the host and parasite phylogenetic histories, the geographical history of the area and a range of ecological processes. In particular, we should expect the presence of phylogenetic signals in the effects of ecological processes on organisms; for example, the influence of solar radiation or habitat productivity on the diversity of different taxa should be more similar among closely related taxa than among distantly related ones. In the context of global change and the risk of emerging diseases, the goal of predicting future biodiversity patterns and species distributions will therefore require a greater integration of possible phylogenetic influences.

We are grateful to Dave Jenkins and Robert Ricklefs for the invitation to contribute to the symposium. We also thank Dave Jenkins, Robert Ricklefs and Felisa Smith for useful comments on an earlier draft, as well as the many collaborators who, over the years, have contributed to our

research on parasite biogeography. This is publication no. 726 of the Mitrani Department of Desert Ecology.

REFERENCES

1 McIntosh, R. 1985 *The background of ecology: concept and theory*. New York, NY: Cambridge University Press.

2 Brooks, D. R. & McLennan, D. A. 1991 *Phylogeny, ecology, and behavior*. Chicago, IL: University of Chicago Press.

3 Schoener, T. W. 1965 The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* **19**, 189–213. (doi:10.2307/2406374)

4 Schoener, T. W. & Gorman, G. C. 1968 Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. *Ecology* **49**, 819–830. (doi:10.2307/1936533)

5 Roughgarden, J. 1974 Niche width: biogeographic patterns among *Anolis* lizard populations. *Am. Nat.* **108**, 429–442. (doi:10.1086/282924)

6 Lomolino, M. V., Riddle, B. R., Whittaker, R. J. & Brown, J. H. 2010 *Biogeography*, 4th edn. Sunderland, MA: Sinauer Associates.

7 Brown, J. H. & Maurer, B. A. 1989 Macroecology: the division of food and space among species on continents. *Science* **243**, 1145–1150. (doi:10.1126/science.243.4895.1145)

8 Brown, J. H. 1995 *Macroecology*. Chicago, IL: University of Chicago Press.

9 Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology*. Oxford, UK: Blackwell Science.

10 Smith, F. A., Lyons, S. K., Ernest, S. K. M. & Brown, J. H. 2008 Macroecology: more than the division of food and space among species on continents. *Prog. Phys. Geog.* **32**, 115–138. (doi:10.1177/0309133308094425)

11 Nee, S. 2002 Thinking big in ecology. *Nature* **417**, 229–230. (doi:10.1038/417229a)

12 Blackburn, T. M. & Gaston, K. J. 2002 Macroecology is distinct from biogeography. *Nature* **418**, 723. (doi:10.1038/418723b)

13 Ruggiero, A. & Hawkins, B. A. 2006 Mapping macroecology. *Glob. Ecol. Biogeogr.* **15**, 433–437. (doi:10.1111/j.1466-822X.2006.00238.x)

14 Blackburn, T. M. & Gaston, K. J. 2006 There's more to macroecology than meets the eye. *Glob. Ecol. Biogeogr.* **15**, 537–540. (doi:10.1111/j.1466-8238.2006.00276.x)

15 Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.

16 Harvey, P. H. 1996 Phylogenies for ecologists. *J. Anim. Ecol.* **65**, 255–263. (doi:10.2307/5872)

17 Ricklefs, R. E. & Starck, J. M. 1996 Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**, 167–172. (doi:10.2307/3545598)

18 Björklund, M. 1994 Are 'comparative methods' always necessary? *Oikos* **80**, 607–612. (doi:10.2307/3546637)

19 Westoby, M., Leishman, M. R. & Lord, J. M. 1995 On misinterpreting the 'phylogenetic correction'. *J. Ecol.* **83**, 531–534. (doi:10.2307/2261605)

20 Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)

21 Jablonski, D. 1987 Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* **238**, 360–363. (doi:10.1126/science.238.4825.360)

22 Peterson, A. T., Soberon, J. & Sanchez-Cordero, V. 1999 Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265–1267. (doi:10.1126/science.285.5431.1265)

23 Qian, H. & Ricklefs, R. E. 2004 Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *J. Ecol.* **92**, 253–265. (doi:10.1111/j.0022-0477.2004.00868.x)

24 Hunt, G., Roy, K. & Jablonski, D. 2005 Species-level heritability reaffirmed: a comment on 'On the heritability of geographic range sizes'. *Am. Nat.* **166**, 129–135. (doi:10.1086/430722)

25 Webb, T. J. & Gaston, K. J. 2003 On the heritability of geographic range sizes. *Am. Nat.* **161**, 553–566. (doi:10.1086/368296)

26 Blackburn, T. M. 2004 Method in macroecology. *Basic Appl. Ecol.* **5**, 401–412. (doi:10.1016/j.baae.2004.08.002)

27 Watters, G. T. 1992 Unionids, fishes, and the species–area curve. *J. Biogeogr.* **19**, 481–490. (doi:10.2307/2845767)

28 Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S. & Degen, A. A. 2004 Relationship between host diversity and parasite diversity: flea assemblages on small mammals. *J. Biogeogr.* **31**, 1857–1866. (doi:10.1111/j.1365-2699.2004.01132.x)

29 Thieltges, D. W., Hof, C., Dehling, D. M., Brändle, M., Brandl, R. & Poulin, R. 2011 Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Glob. Ecol. Biogeogr.* (doi:10.1111/j.1466-8238.2010.00631.x)

30 Zamparo, D., McLennan, D. A. & Brooks, D. R. 1999 Macroevolutionary patterns of male reproductive investment in a clade of parasitic hermaphrodites. *J. Parasitol.* **85**, 540–544. (doi:10.2307/3285792)

31 Morand, S., Legendre, P., Gardner, S. L. & Hugot, P. 1996 Body size evolution of oxyurid (Nematoda) parasites: the role of hosts. *Oecologia* **107**, 274–282. (doi:10.1007/BF00327912)

32 Poulin, R. 1996 The evolution of life history strategies in parasitic animals. *Adv. Parasitol.* **37**, 107–134. (doi:10.1016/S0065-308X(08)60220-1)

33 Randhawa, H. S. & Poulin, R. 2009 Determinants and consequences of interspecific body size variation in tetraphyllidean tapeworms. *Oecologia* **161**, 759–769. (doi:10.1007/s00442-009-1410-1)

34 Poulin, R. & Combes, C. 1999 The concept of virulence: interpretations and implications. *Parasitol. Today* **15**, 474–475. (doi:10.1016/S0169-4758(99)01554-9)

35 Thomas, F., Renaud, F., Rousset, F., Cézilly, F. & De Meeüs, T. 1995 Differential mortality of two closely related host species induced by one parasite. *Proc. R. Soc. Lond. B* **260**, 349–352. (doi:10.1098/rspb.1995.0103)

36 Jaenike, J. 1996 Suboptimal virulence of an insect-parasitic nematode. *Evolution* **50**, 2241–2247. (doi:10.2307/2410694)

37 Vickery, W. L. & Poulin, R. 1998 Parasite extinction and colonization and the evolution of parasite communities: a simulation study. *Int. J. Parasitol.* **28**, 727–737. (doi:10.1016/S0020-7519(98)00036-8)

38 Poulin, R. 1995 Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol. Monogr.* **65**, 283–302. (doi:10.2307/2937061)

39 Cooper, N., Jetz, W. & Freckleton, R. P. 2010 Phylogenetic comparative approaches for studying niche conservatism. *J. Evol. Biol.* **23**, 2529–2539. (doi:10.1111/j.1420-9101.2010.02144.x)

40 Blomberg, S. P., Garland Jr, T. & Ives, A. R. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)

41 Abouheif, E. 1999 A method for testing the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.* **1**, 895–909.

42 Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)

43 Pavoine, S., Ollier, S., Pontier, D. & Chessel, D. 2008 Testing for phylogenetic signal in phenotypic traits: new matrices of phylogenetic proximities. *Theor. Popul. Biol.* **73**, 79–91. (doi:10.1016/j.tpb.2007.10.001)

44 Krasnov, B. R., Poulin, R. & Mouillot, D. 2011 Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. *Ecography* **34**, 114–122. (doi:10.1111/j.1600-0587.2010.06502.x)

45 Nabout, J. C., Terribile, L. C., Bini, L. M. & Diniz-Filho, J. A. F. 2009 Phylogenetic autocorrelation and heritability of geographic range size, shape and position of fiddler crabs, genus *Uca* (Crustacea, Decapoda). *J. Zool. Syst. Evol. Res.* **48**, 102–108. (doi:10.1111/j.1439-0469.2009.00531.x)

46 Mouillot, D., Krasnov, B. R., Shenbrot, G. I., Gaston, K. J. & Poulin, R. 2006 Conservatism of host specificity in parasites. *Ecography* **29**, 596–602. (doi:10.1111/j.0906-7590.2006.04507.x)

47 Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S. & Poulin, R. 2004 Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. *Ecography* **27**, 787–797. (doi:10.1111/j.0906-7590.2004.04015.x)

48 Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)

49 Garland Jr, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

50 Martins, E. P. & Hansen, T. F. 1997 Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149**, 646–667. (doi:10.1086/286013)

51 Pagel, M. 1997 Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. *J. Theor. Biol.* **164**, 191–205. (doi:10.1006/jtbi.1993.1148)

52 Gage, M. J. G. & Freckleton, R. P. 2003 Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. *Proc. R. Soc. Lond. B* **270**, 625–632. (doi:10.1098/rspb.2002.2258)

53 Freckleton, R. P. 2009 The seven deadly sins of comparative analysis. *J. Evol. Biol.* **22**, 1367–1375. (doi:10.1111/j.1420-9101.2009.01757.x)

54 Ives, A. R. & Garland Jr, T. 2010 Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.* **59**, 9–26. (doi:10.1093/sysbio/syp074)

55 Jombart, T., Pavoine, S., Devillard, S. & Pontier, D. 2010 Putting phylogeny into the analysis of biological traits: a methodological approach. *J. Theor. Biol.* **264**, 693–701. (doi:10.1016/j.jtbi.2010.03.038)

56 Martins, E. P., Diniz-Filho, J. A. F. & Housworth, E. A. 2002 Adaptive constraints and the phylogenetic comparative method: a computer simulation test. *Evolution* **56**, 1–13. (doi:10.1111/j.0014-3820.2002.tb00844.x)

57 Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S., Mouillot, D. & Poulin, R. 2008 Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *J. Biogeogr.* **35**, 592–601. (doi:10.1111/j.1365-2699.2007.01800.x)

58 Legendre, P., Lapointe, F.-J. & Casgrain, P. 1994 Modeling brain evolution from behavior: a permutational regression approach. *Evolution* **48**, 1487–1499. (doi:10.2307/2410243)

59 Diniz-Filho, J. A. F., de Sant'Ana, C. E. R. & Bini, L. M. 1998 An eigenvector method for estimating phylogenetic inertia. *Evolution* **52**, 1247–1262. (doi:10.2307/2411294)

60 Lichstein, J. W. 2007 Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol.* **188**, 117–131. (doi:10.1007/s11258-006-9126-3)

61 Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S. & Poulin, R. 2010 Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. *Glob. Ecol. Biogeogr.* **19**, 515–526. (doi:10.1111/j.1466-8238.2010.00529.x)

62 Hafner, M. S. & Nadler, S. A. 1988 Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* **332**, 258–259. (doi:10.1038/332258a0)

63 Poulin, R. 2007 *Evolutionary ecology of parasites*, 2nd edn. Princeton, NJ: Princeton University Press.

64 Morand, S. & Poulin, R. 2003 Phylogenies, the comparative method and parasite evolutionary ecology. *Adv. Parasitol.* **54**, 281–302. (doi:10.1016/S0065-308X(03)54006-4)

65 Poulin, R. & Mouillot, D. 2003 Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* **126**, 473–480. (doi:10.1017/S0031182003002993)

66 Bush, A. O. & Kennedy, C. R. 1994 Host fragmentation and helminth parasites: hedging your bets against extinction. *Int. J. Parasitol.* **24**, 1333–1343. (doi:10.1016/0020-7519(94)90199-6)

67 Poulin, R. & Morand, S. 2004 *Parasite biodiversity*. Washington, DC: Smithsonian Institution Press.

68 Krasnov, B. R., Poulin, R., Shenbrot, G. I., Mouillot, D. & Khokhlova, I. S. 2004 Ectoparasitic 'jacks-of-all-trades': relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. *Am. Nat.* **164**, 505–516. (doi:10.1086/423716)

69 Eeley, H. A. C. & Foley, R. A. 1999 Species richness, species range size and ecological specialization among African primates: geographical patterns and conservation implications. *Biodivers. Conserv.* **8**, 1033–1056. (doi:10.1023/A:1008831320469)

70 Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279. (doi:10.1086/284267)

71 Krasnov, B. R., Poulin, R., Shenbrot, G. I., Mouillot, D. & Khokhlova, I. S. 2005 Host specificity and geographic range in haematophagous ectoparasites. *Oikos* **108**, 449–456. (doi:10.1111/j.0030-1299.2005.13551.x)

72 Stevens, G. C. 1989 The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256. (doi:10.1086/284913)

73 Willig, M. R., Kaufman, D. M. & Stevens, R. D. 2003 Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309. (doi:10.1146/annurev.ecolsys.34.012103.144032)

74 Vázquez, D. & Stevens, R. D. 2004 The latitudinal gradient in niche breadth: concepts and evidence. *Am. Nat.* **164**, E1–E19. (doi:10.1086/421445)

75 Ruggiero, A. & Werenkraut, V. 2007 One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Glob. Ecol. Biogeogr.* **16**, 401–414. (doi:10.1111/j.1466-8238.2006.00303.x)

76 Letcher, A. J. & Harvey, P. H. 1994 Variation in geographical range size among mammals of the Palaearctic. *Am. Nat.* **144**, 30–42. (doi:10.1086/285659)

77 Hernández Fernández, M. & Vrba, E. S. 2005 Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *J. Biogeogr.* **32**, 903–918. (doi:10.1111/j.1365-2699.2004.01188.x)

78 Esch, G. W., Kennedy, C. R., Bush, A. O. & Aho, J. M. 1988 Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology* **96**, 519–532. (doi:10.1017/S003118200008015X)

79 Criscione, C. D. & Blouin, M. S. 2004 Life cycles shape parasite evolution: comparative population genetics of salmon trematodes. *Evolution* **58**, 198–202.

80 Thieltges, D. W., Hof, C., Borregaard, M. K., Dehling, D. M., Brändle, M., Brandl, R. & Poulin, R. 2011 Range size patterns in European freshwater trematodes. *Ecography.* (doi:10.1111/j.1600-0587.2010.06268.x)

81 Poulin, R. 2003 The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *J. Biogeogr.* **30**, 1609–1615. (doi:10.1046/j.1365-2699.2003.00949.x)

82 Fellis, K. J. & Esch, G. W. 2005 Variation in life cycle affects the distance decay of similarity among bluegill sunfish parasite communities. *J. Parasitol.* **91**, 1484–1486. (doi:10.1645/GE-578R.1)

83 Krasnov, B. R., Shenbrot, G. I., Mouillot, D., Khokhlova, I. S. & Poulin, R. 2005 Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographic distance or faunal similarity? *J. Biogeogr.* **32**, 633–644. (doi:10.1111/j.1365-2699.2004.01206.x)

84 Brouat, C. & Duplantier, J. M. 2007 Host habitat patchiness and the distance decay of similarity among gastro-intestinal nematode communities in two species of *Mastomys* (southeastern Senegal). *Oecologia* **152**, 715–720. (doi:10.1007/s00442-007-0680-8)

85 Thieltges, D. W., Ferguson, M. A. D., Jones, C. S., Krakau, M., de Montaudouin, X., Noble, L. R., Reise, K. & Poulin, R. 2009 Distance decay of similarity among parasite communities of three marine invertebrate hosts. *Oecologia* **160**, 163–173. (doi:10.1007/s00442-009-1276-2)

86 Pérez-del-Olmo, A., Fernández, M., Raga, J. A., Kostadinova, A. & Morand, S. 2009 Not everything is everywhere: the distance decay of similarity in a marine host–parasite system. *J. Biogeogr.* **36**, 200–209. (doi:10.1111/j.1365-2699.2008.02000.x)

87 Soininen, J., McDonald, R. & Hillebrand, H. 2007 The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

88 Vinarski, M. V., Korallo, N. P., Krasnov, B. R., Shenbrot, G. I. & Poulin, R. 2007 Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host species composition or environment? *J. Biogeogr.* **34**, 1691–1700. (doi:10.1111/j.1365-2699.2007.01735.x)

89 Poulin, R., Blanar, C. A., Thieltges, D. W. & Marcogliese, D. J. 2011 The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance. *Ecography.* (doi:10.1111/j.1600-0587.2010.06826.x)

90 Poulin, R. & Krasnov, B. R. 2010 Similarity and variability of parasite assemblages across geographical space. In *The biogeography of host–parasite interactions* (eds S. Morand & B. R. Krasnov), pp. 115–127. Oxford, UK: Oxford University Press.

91 Poulin, R., Guilhaumon, F., Randhawa, H. S., Luque, J. L. & Mouillot, D. 2011 Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* **120**, 740–747. (doi:10.1111/j.1600-0706.2010.19036.x)

92 Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S., Vinarski, M. V., Korallo-Vinarskaya, N. P. & Poulin, R. 2010 Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: which matters the most? *Int. J. Parasitol.* **40**, 807–817. (doi:10.1016/j.ijpara.2009.12.002)