15 Comparative phylogeography: The use of parasites for insights into host history

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1 Introductory remarks

Parasites are useful biological tags of the ecology of their hosts. In this chapter, we will show that parasites can also be used as powerful “evolutionary prints” in order to generate new hypotheses about the history of their hosts. By this we mean that genes of a parasite might actually better reflect host history than genes of the host. This can be useful as incongruence between the genealogies of several genes within a species often limits the resolution of the species history. We will focus on the developing field of comparative phylogeography between hosts and parasites and show that parasites can highlight historical events affecting host lineages that can not be detected by the study of the host itself, such as past host migration or differentiation events. Congruence in host-parasite phylogeographies relies on long-term host specificity, which is favoured by limited dispersal abilities, direct life cycles, high abundance and prevalence of the parasite. Parasites might play the role of an evolutionary print of their host’s history if they present reduced ancestral polymorphism, i.e. when parasites have shorter generation times and lower effective sizes than their hosts. Provided that the appropriate parasite species is selected according to these conditions, there appears to be no limitation to the use of parasites as evolutionary prints of the phylogeography of their hosts.

2 Parasites as prints of their hosts in evolutionary biology

The number of extant parasite species is estimated to represent ~30% of the biodiversity of eukaryote species and ~10% of currently known species of Metazoa (DeMeeûs and Renaud 2003; Poulin and Morand 2004). Parasites have been shown to be useful sources of information about various aspects of the ecology of their hosts. For example, parasites can be used as ecological tags to provide insights into different life-history traits of their hosts; parasitic species are used as biological tags to discriminate stocks, migration routes and nursery grounds of commercially exploited marine fish populations (Olson and Pratt 1973; Bouillon and Dempson 1989; Mackenzie 2002). Parasites can also help monitor accurately the health of the host ecosystem and human impacts on that environment, as the tissues of some acanthocephalan and cestode species accumulate up to 2700 times more heavy metal compounds compared with the tissues of their final hosts (Sures 2004).

Whereas most current studies focus on extant host-parasite relationships, parasites can also be used as "evolutionary prints" to better characterize the evolutionary history of their hosts (Thomas et al. 1996; Nieberding et al. 2004; Whiteman and Parker 2005). Indeed, parasites are unique in that their evolutionary history is tightly influenced by their intimate relationships with their hosts (Nadler 1995). As a correlate, it can be assumed that the genetic structure of parasites might be generated by the evolutionary history of their hosts. Provided that hosts and parasites share a common history of speciation, comparing the genetic structure of parasites with that of their hosts could provide information about the evolutionary history of the host that is not detectable by studying the host directly (Thomas et al. 1996; Nieberding et al. 2004). Parasites could therefore be used to reveal cryptic traits of the evolutionary history of their hosts (as a biological "magnifying glass" effect). This approach has been used successfully in several evolutionary biology studies. For example, parasitological data from hybrid or contact zone populations of the hosts have been used to detect host hybrids and to quantify gene flow among host lineages (Cloutman 1988; Moulia et al. 993; Hafner et al. 1998; Derothe et al. 2001). In other studies, comparison of the phylogenies of hosts with those of their specific parasites has allowed researchers to better understand relationships among host species, and to detect the existence of cryptic host species (Thomas et al. 1996; Haukisalmi et al. 2001).

Recently, it was suggested that the parasite magnifying glass effect could prove highly useful in the field of phylogeography: by comparing phylogeographical data from parasites with that of their hosts, one could reveal cryptic phylogeographical traits of the hosts, i.e. cryptic historical gene flow or differentiation events between host lineages. Here we give first a general overview of the increasing number of studies comparing host-parasite phylogeographies, highlighting how the genetic structure of the parasite gave insight into its host phylogeography. Second, we examine the traits of the host and the parasite that can determine whether the phylogeographies of parasites can act as magnifying glasses of the evolutionary history of their hosts. We also provide an overview of the host-parasite characteristics that should be considered to select a parasite useful as a biological magnifying glass of its host.

3 Case studies in host-parasite comparative phylogeography

An increasing number of studies have identified new phylogeographical traits of different host species based on the analysis of the phylogeographical pattern of their parasites. These included the identification of cryptic host lineages, Quaternary refuges, migration routes or migration epochs, and past gene flow between host populations. In contrast, similar other studies have failed to show any magnifying glass effect of the parasite. These different studies are described briefly below.

3.1 Cryptic contacts among host lineages

The phylogeography of the modern human louse *Pediculus humanus* reveals that the species is formed by two ancient lineages that co-diverged 0.7 to 1.2 Myrs ago. As both *P. humanus* lineages have the same ecological niche, they must have diverged in allopatry on ancient *Homo* populations. The presence of both louse lineages on modern humans strongly suggests that a direct physical contact existed between archaic and modern lineages of *Homo* (Reed et al. 2004).

3.2 Cryptic host refuges during the Quaternary cold stages

The phylogeographical patterns of the bast scale *Matsucoccus feytaudi* and of its specific host, the maritime pine *Pinus pinaster*, were compared over the Mediterranean region (Burban et al. 1999; Burban and Petit 2003). Both species display near congruent genetic and geographical groups in Western Europe, along the European Atlantic coast and in North Africa. The phylogeography of *M. feytaudi* revealed the presence of a cryptic evolutionary unit in Punta Cires (Morocco) and multiple cryptic refuges in the Iberian refuge during ice ages from which northward European recolonisation occurred for both host and parasite species.

3.3 Cryptic epochs and routes of host migrations

The phylogeographical patterns of the nematode *Heligmosomoides polygyrus* and its rodent host, *Apodemus sylvaticus*, were compared across Europe. Both species co-differentiated in southwest Europe, North Africa, Italy and on seven Mediterranean islands (Nieberding et al. 2004, 2005, 2006). Moreover, the parasite phylogeography revealed (a) the existence of supplementary distinct allopatric refuges in Iberia and Italy for both species during the Quaternary; (b) that the colonisation of North Africa occurred from southern Spanish populations in both species; and (c) that occasional contacts persisted between the Sicilian and southern Italian populations of both species until ~200 000 years after the differentiation of host populations (Fig. 1).

The umbelliferous *Bowlesia incana* has currently a disjunctive distribution north and south of the tropical regions of Central America. The phylogeography of its herbivore butterfly parasite *Greya powelli* showed that the introduction of *B. incana* in North America from South America was several orders of magnitude older than was previously thought (250 years) (Pellmyr et al. 1998). Similarly, the phylogeographical pattern of *Puumala* hantaviruses (PUUV) across Europe and Russia confirmed the accuracy of one of the two immigration routes proposed for its host, the bank vole *Clethrionomys glareolus* across the Russian plain towards Fennoscandia at the end of the last glacial period (Asikainen et al. 2000; Dekonenko et al. 2003).

3.4 Cryptic host lineages

The phylogeographical structure of the parasitic angiosperm *Arceuthobium americanum* and of its conifer *Pinus* hosts were compared in north-western America (Jerome and Ford 2002a, b). Three genetic races of *A. americanum* each parasitize specifically one allopatric host lineage. This revealed the accuracy of host taxonomic differentiation into *P. contorta* var. *latifolia* and var. *murrayana* and *P. banksania*, in spite of low host genetic and morphological differentiation among them.

3.5 Incongruent phylogeographies

In spite of the many examples of parasite phylogeographies matching closely those of their host, there are also examples where matches do not occur. The phylogeographical patterns of *Greya* butterflies were broadly compared across America with those of their Saxifragacea host plants and their parasitoid wasps *Agathis* (Brown et al. 1997; Althoff and Thompson. 1999). The generalist *Greya politella*, which has achieved numerous host species shifts over its recent evolutionary history, has a phylogeographical pattern showing no co-differentiation with a particular host. Similarly, the phylogeographical structures of the generalist parasitoid wasps *Agathis thompsoni* and *Agathis nsp*. are incongruent with those of their main hosts *G. subalba* and *G. enchrysa*.

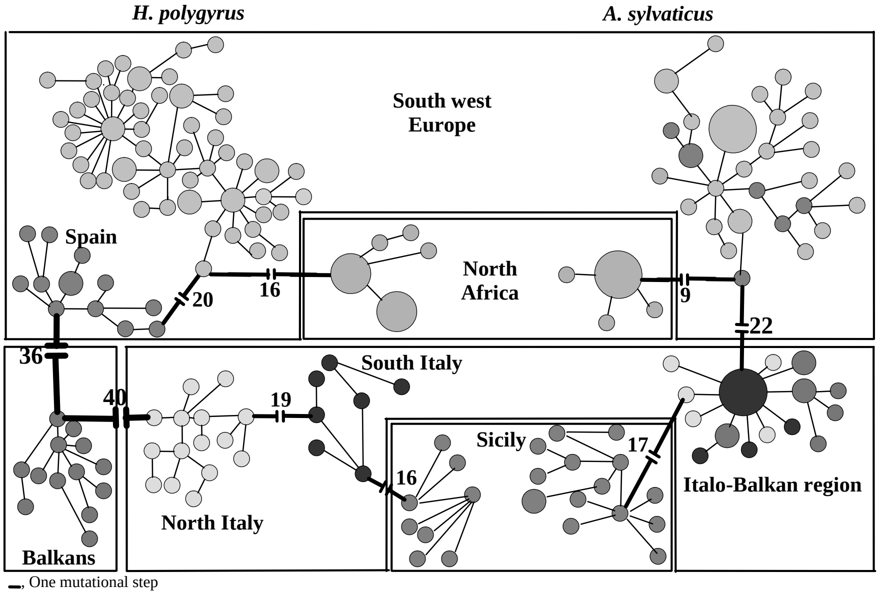

Fig. 1. Minimum spanning networks of the nematode *H. polygyrus* (on the left) and its host, the woodmouse *A. sylvaticus* (on the right), on the basis of cytochrome b gene sequences. Branch lengths correspond to the number of mutational steps (given in bold characters) separating haplotypes, represented by circles. Populations from Spain, southwest Europe, North Africa, the Balkan region, north Italy, south Italy and Sicily, are compared in both species. Partial congruence is observed because both species present a south west European, a north African, an Italian and a Sicilian clade, linked by a high number of mutational steps. However, partial incongruence between the networks of both species is also observed: (a) *H. polygyrus* Italian and Balkan populations form two distinct clades, and (b) *H. polygyrus* Italian and south west European are further divided into several subclades, although the corresponding host populations cannot be distinguished. These particular (sub)clades in *H. polygyrus* highlight the fact that the phylogeography of the parasite is more diversified, differentiated than that of its host (modified from Nieberding et al. 2004)

Similarly, the Australian brood-parasite Horsfield’s bronze-cuckoo *Chalcites basalis* lays eggs in the nests of its hosts, *Malurus* fairy-wrens and *Acanthiza* thornbills. The lack of phylogeographical structure of *C. basalis* denies the existence of evolutionarily long-term stable host races in this species, which is likely to have expanded its geographical and host species range within the past few tens of thousands of years, following climatic amelioration during the late Pleistocene (Joseph et al. 2002).

The phylogeographies of the cestode *Paranoplocephala arctica* and of its lemming *Dicrostonyx* hosts were compared over the Holarctic region (Wickstrom et al. 2003). Both taxa present two differentiated clades in the Nearctic and Palearctic regions, separated by the Bering Strait. However, the parasite phylogeography presents additional differentiation events on Wrangle Island around the Bering Strait and on Canadian Artic islands that do not reflect the phylogeography of the host lemming. The discrepancies between *P. arctica* and *Dicrostonyx* could be due to the passage of *P. arctica* through intermediate soil invertebrate hosts, which could reduce dependence on a definitive lemming host.

4 Common traits in hosts and parasites displaying co-differentiating phylogeographies

Here we examine the life-history traits and other features of the host and the parasite that might help determine whether the phylogeographies of parasites can act as magnifying glasses of the evolutionary history of their hosts.

4.1 Congruence versus incongruence

A survey of the existing host-parasite comparative phylogeographies highlights that parasites can indeed reveal cryptic evolutionary events of their host, such as the existence of past cryptic migration or differentiation events, and of past cryptic refuges or lineages across the last few millions years.

Moreover, these studies also provide clues to understand how and why co-differentiation occurs on a phylogeographical evolutionary timescale (i.e. a few million years). Indeed, the congruence in host-parasite phylogeographies discussed above appears to be determined by the duration and degree of intimacy of host and parasite relationships, i.e. long-term host specificity (Johnson et al. 2003). Long-term host specificity should indeed limit *host switching* opportunities (Blouin et al. 1995). As a correlate, the absence of long-term host-parasite specificity explains most incongruent host-parasite phylogeographies: the phylogeographies of generalist parasites are not related to those of their hosts (Althoff and Thompson 1999; Brown et al. 1997; Joseph et al. 2002). Similarly, intermediate hosts in the parasite life cycle reduce the congruence of the parasite with the phylogeographical history of the definitive host (Wickstrom et al. 2003).

Table 1. Survey of the host-parasite congruent comparative phylogeographies according to the following traits of the parasites: dispersal ability, reproduction mode, prevalence and abundance. Importantly, in all the studies cited, the level of host specificity is high and the life cycle is direct (no intermediate host) for the parasite

Host	Parasite	Geographic distribution	Parasite dispersal ability	Parasite reproduction mode	Prevalence, abundance
PLANTS					
Pinus pinaster	*Matsucoccus feytaudi*	Mediterranean region	Higher than its host	Sexual	Variable
P. contorta, *P. banksania*	*Arceuthobium americanum*	North-West America	Lower than its host	Sexual	High
Bowlesia incana	*Greya powelli*	Nearctic region	Lower than its host	Sexual	High
ANIMALS					
Apodemus sylvaticus	*Heligmosomoides polygyrus*	Europe	Lower than its host	Sexual	High
Clethrionomys glareolus	*Hantavirus*	Palearctic region	Lower than its host	Clonal	High
Homo sapiens	*Pediculus humanus*	Worldwide	Lower than its host	Sexual	High

Host-parasite species pairs showing congruent phylogeographies appear to share common life-history, ecological, or demographic traits that favour long-term host specificity (Table 1). A direct life cycle of the parasite (i.e. no intermediate host) is one important trait shared by congruent host-parasite phylogeographies. This trait makes the gene flow of the parasite determined primarily by the contacts and movements of its host, which limits failure of the parasite to speciate in response to host speciation, i.e.

parasite release (Johnson et al. 2003). In addition, high abundance and high prevalence of the parasite on or within its host reduces the risks of *parasite extinction* and of "*missing the boat*" (Clayton et al. 2003). Together, these three factors increase the probability that a parasite matches the differentiation of its host and the probability that congruent host-parasite phylogeographies are observed.

4.1.1 Reproductive mode

Parasite sexual reproduction maintains gene flow between populations because adults have to meet in/on the host in order to produce the next generation. By contrast, parasite parthenogenetic and clonal reproduction induce genetic drift among populations, because adult individuals do not need to meet to produce the next generation (Gow et al. 2004). Therefore, sexually reproducing parasites should better follow the mixing of their host populations and consequently better reflect their history of differentiation or migration events. This will limit the risk that the parasite does not speciate in response to host speciation. An example is given by the nematode *H. polygyrus* parasitizing the wood mouse *A. sylvaticus*: gene flow between *H. polygyrus* populations depends on that of *A. sylvaticus*, which favoured the partial congruence observed between the phylogeographies of both species (Nieberding et al. 2004, 2005, 2006).

4.1.2 Abundance and prevalence

Levels of prevalence and abundance of parasite species also determine the congruence level in host-parasite phylogeographies, because parasite populations whose abundance and prevalence are high in their hosts have a better probability to follow migration and differentiation events between host populations, reducing the probability of parasite extinction.

4.2 Parasites as a "biological magnifying glass"

Although incongruent host-parasite phylogeographies are useful for better understanding the dynamics of host-parasite specificity, these studies can not reveal anything about cryptic historical host events, because the phylogeographical history of the parasite was not generated by the evolutionary history of its current host. Therefore, (partial) congruent host-parasite phylogeographies are a prerequisite for the use of parasites as evolutionary prints. In other words, similar geographical and genetic groups must be present in the corresponding host and parasite populations, and result from the same historical events.

Current studies inferring hypotheses on past historical events of a focal species on the basis of the history of one of its symbiont usually lack an estimation of temporal congruence between the phylogeographical data of the interacting species. However, the presence in host and parasite phylogeographies of similar geographic lineages (spatial congruence) does not necessarily imply real host and parasite historical co-differentiation because similar geographic patterns do not obligatorily result from the same historical events. Therefore, in order to assess co-differentiation, it is necessary to show that similar geographic lineages in the host and its parasite differentiated simultaneously in the past and therefore display temporal congruence of their phylogeographies (Page 2003). This requires the dating of the epoch of differentiation of lineages of both organisms. However, it is generally not possible to directly quantify the absolute rate of molecular evolution of parasite lineages, as parasites generally do not display fossil records. In order to fill this methodological gap, a method was recently proposed to estimate the level temporal congruence between host and parasite lineages (Box 1).

In case of host-parasite (partial) congruence, parasites might display a biological magnifying glass effect, providing information about the evolutionary history of the host that is not detectable at the host level. This is possible if the phylogeography of the parasite is more diversified than that of its host. The genetic diversification of a species is a balance between genetic drift and gene flow: genetic drift counteracts the effects of gene flow by eroding genetic diversity within populations and by increasing differentiation between them (Gow et al. 2004). Consequently, a parasite should present lower gene flow and higher genetic drift between populations than its host in order to act as an evolutionary print of its host. Gene flow and genetic drift appear to be determined primarily by the dispersal ability, the effective population size (N_e), and the DNA mutation rate (μ) of the species (Frankham 2002). From a macroevolutionary perspective, this would promote parasite speciation in the absence of host speciation, i.e. duplication events (Clayton et al. 2003).

4.2.1 Dispersal ability

A lower dispersal ability of the parasite compared with that of its host is likely to be one important factor favouring a higher genetic differentiation between parasite populations, in comparison with its corresponding host populations. Indeed, several studies devoted to the comparison of host-parasite population genetics reveal that high dispersal ability of the parasite homogenizes its population structure (McCoy et al. 2003; Baer et al. 2004), whereas lower dispersal ability enhances local differentiation of the parasite (Blouin et al. 1995; Johnson et al. 2002; Reed and Hafner. 1997; Bohonak. 1999; Bucheli et al. 2001). For example, a lack of congruence is observed between the phylogeographies of the liver fluke *Fascioloides magna* and its specific deer host *Odocoileus virginianus* in northwest America. In this system, the long-distance dispersal of the parasite counteracted local differentiation of its host populations (Mulvey et al. 1991). By contrast, the deer intestinal nematode *Mazamastrongylus odocoilei*, with limited dispersal abilities, presents substantial population differentiation (Blouin et al. 1995). Therefore, the lower dispersal abilities of parasites compared with those of their hosts is a key factor that enables them to represent an evolutionary print of their host.

4.2.2 Effective population size (N_e)

Low parasite N_e increases genetic drift, which in turn increases the probability that the parasite will play the role of a magnifying glass in its host phylogeography. Low prevalence, low abundance and parthenogenetic reproduction are three important factors that reduce N_e in parasites (Anderson et al. 1998; Blouin et al. 1998). For example, the parthenogenetic nematode *Heterorhabditis marelatus* parasitizing soil-dwelling insects in America has a low N_e which has led to high population differentiation (Blouin et al. 1999). However, as high values of prevalence and abundance of parasite species also determine the congruence level in host-parasite phylogeographies by reducing the risks of parasite extinction and of “missing the boat”, intermediate levels of prevalence and abundance should be the appropriate compromise to detect a biological magnifying glass effect of the parasite in the phylogeography of its host.

4.2.3 DNA mutation rate

Accelerated substitution rate in the parasite DNA in comparison to homologous genes of their hosts make parasites ideal independent markers of their hosts because they would amplify the evolutionary history of their hosts in their genes (Blouin et al. 1995; Whiteman and Parker 2005). For example, in the *A. sylvaticus* - *H. polygyrus* host-parasite system, the rate of molecular evolution of the cytochrome b gene is ~1.5 fold higher in the parasite than in its host (Nieberding et al. 2004). This result agrees with those of other host-parasite studies that found a faster rate of molecular evolution in parasitic genes compared with the homologous genes of their specific hosts (Hafner et al. 1994; Page et al. 1998; Paterson et al. 2000).

Box 1. In order to assess whether similar geographic lineages in the host and the parasite differentiated simultaneously in the past (temporal congruence), one method consists of plotting the genetic distances between pairs of host individuals and pairs of parasite individuals, such that each parasite must be related to a host from the same population (see Page 2003 for more details). In case of significant historical codivergence between host and parasite lineages, a linear correlation is observed between the genetic distances of pairs of hosts and pairs of corresponding parasites, and the y-intercept of the resulting correlation line passes through the origin (0,0). If a correlation line is observed but its y-intercept is significantly different from zero, this means that the parasite lineages differentiated before or after the host lineages. This method can be applied to both sequence or multiloci genetic data. In case of sequence data, this methodology was successfully applied to show significant codivergence between *H. polygyrus* and *A. sylvaticus* phylogeographies over south west Europe, using the program TreeMap (Page 1994; Nieberding 2004). Interestingly, if temporal congruence is assessed, the absolute rate of parasite molecular evolution can then be estimated on the basis of the host molecular data, provided that homologous genes were sequenced in both organisms (Avise 2000). In contrast to sequence data, multi loci data (AFLP, RFLP, or microsatellites) can also be used to estimate temporal congruence between host and parasite lineages (Beaumont 2005). Assuming mutation and migration are low, pairwise Fst among populations or individuals can be used as an estimator of the level of genetic differentiation between populations (Rousset 1997; Bohonak 1999). Therefore, the correlation between the genetic structures of two organisms can be estimated using Mantel tests on pairwise genetic distance matrices, using Fst/(1-Fst) values. The program CADM (congruence among distance matrices (Legendre and Makarenkov 2002) allows statistical comparison of full distance matrices. Significance of the Mantel test can then be assessed over large number (e.g., 10000) of permutations. Similarly to sequence data, temporal congruence will be confirmed if a correlation line passing through (0,0) is observed. This methodology has been applied successfully (Jerome 2002b; Anderson et al. 2004).

5 Conclusions and perspectives

Incongruence among gene genealogies within a single species is often observed, and can be due to (a) differences in evolutionary processes, (b) differences in history, or (c) sampling error (reviewed in Nichols 2001). This limits the confidence we can have in the results or the resolution of the organism's history. Recent studies have thus considered the possibility that genes of other, unrelated organisms might actually provide a better picture of the history of the focal organism. These studies showed that indeed gene trees of other, symbiotic, organisms might actually better reflect the true history of a given (focal) organism, compared to gene trees of the focal organism itself (see Whiteman and Parker 2005 for a review in the context of animal parasites and conservation)

This idea is currently emerging in comparative phylogeography. Even if additional studies are needed to better characterize and quantify the relative effects of the different traits discussed here and to identify possible new ones, it appears that numerous studies have already shown the utility and sensitivity of this approach: parasites can successfully be used to generate new hypotheses about the phylogeographic history of their hosts, highlighting possible cryptic historical gene flow, differentiation events, host refuges and lineages, which could not be detected by the phylogeographical study of the host itself.

When focusing on micro-mammal hosts and their macro-parasites, helminths as endoparasites, ticks and lice as ectoparasites have been the most regularly used parasite tags in wild host-parasite comparative phylogeographies (Anderson et al. 1998; Blouin et al. 1995, 1998, 1999; Clayton et al. 2003; Johnson et al. 2003; McCoy et al. 2003; Nieberding et al. 2004; Wickstrom et al. 2003). These parasitic groups have proved to be highly useful as these taxa are harbored by every micro-mammal and present a rapid rate of molecular evolution (Page et al. 1998; Johnson et al. 2003; Nieberding et al. 2004). However, there should be no taxonomic limitation to the use of other macro-parasites as evolutionary prints of the phylogeography of their micro-mammal hosts, provided that the parasite species is selected according to the life history traits and other features mentioned in this review. The appropriate parasite should display current host specificity, a direct life cycle, as well as high abundance and prevalence levels on its host, in order to favour long-term host-parasite specificity. Moreover, the dispersal ability of the selected parasite should be limited by that of its host, while its effective population size and molecular mutation rate should be respectively lower and higher than those of its host. Provided that the appropriate parasite species is chosen according to these conditions, there appears to be no limitation to the use of microparasites as evolutionary prints of the phylogeography of their micromammal hosts.

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