CHAPTER 2

Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology

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Recent insights into both population and community ecology of host-parasite relationships have shown the importance of spatial processes in influencing the structure of local parasite and microbe communities. This now requires from parasitologists, epidemiologists and evolutionary biologists working on those interactions that they place their analyses into a broader spatial perspective. Because local species richness and composition in parasites and pathogens depend on large-scale species pools, a greater consideration of epidemiological processes will favour the emergence of spatial parasitology and epidemiology devoted to understanding population dynamics and community structure.

2.1 Introduction

There is an increasing interest in parasite and infectious disease population (Grenfell and Dobson 1995; Hudson *et al.* 2001) and community (Esch *et al.* 1990; Poulin 1998*a*; Rohde 2001) ecology, and interestingly this has developed at a time when mainstream ecologists have shown increasing interest in metapopulation theory and habitat fragmentation (Hanski and Gilpin 1997; Hanski 1999), population dynamics in fragmented landscape (Hassell and Wilson 1997; Ferguson *et al.* 1997; Grenfell and Harwood 1997; Rohani *et al.* 1999) and macroecology (Brown 1995; Rosenzweig 1995; Maurer 1999; Lawton 2000; Gaston and Blackburn 2000). The development of what is now called spatial ecology is one of the great triumphs of modern population and community ecology (Tilman and Kareiva 1997), which has showed the critical importance of space and spatial characteristics for understanding a wide range of ecological phenomena (Holt 1993, 1999). There are clear analogies between modern spatial ecology and parasite–infectious disease population and community ecology, and this chapter will be devoted to a review of the recent development in parasite–infectious disease population and community ecology within this fruitful cross-fertilizing arena.

There are considerably more studies available on parasitic systems today than 10 years ago (see Poulin 1997, 1998*a*; Poulin *et al.* 2000 for a review), and many of these investigations have clearly showed the role of dynamical processes in a spatial context (Ferguson *et al.* 1997; Grenfell and Harwood 1997; Morand and

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Guégan 2000*a*; Poulin and Guégan 2000; Morand *et al.* 2002). Most if not all parasites live as populations that are divided into metapopulations on several spatial scales, and each host operates as a patch. Many of the topics in modern spatial ecology have also their parallels in within-host infection processes with the individual host body forming an heterogeneous environment (see Holt 1999). From the perspective of a parasitic larval form or microbe, an individual host is an extraordinary landscape to invade with heterogeneity in resource availability and colonization-extinction risks. An infrapopulation is thus defined as all the members of a given parasite species within a single host individual, and an infracommunity includes all of the infrapopulations within an individual host. The next hierarchical level includes all the infrapopulations sampled from a given host species within an ecosystem, and which forms the metapopulation. Parallel to the metapopulation is the component parasite community which represents all of the infracommunities within a given host population. Then the highest level of parasite organization is the suprapopulation which represents all individuals of a given parasite species within an ecosystem. Next, the parasite compound community consists of all the parasite communities within an ecosystem (see Esch *et al.* 1990). This creates at least a third-order scaling of habitat fragmentation for the parasites which has a significant impact on the development of theory regarding the evolution of populations and communities of parasites and pathogens. Infrapopulations and infracommunities may form many replicates from one host to another, thus providing a remarkable opportunity for comparative analyses of the variability of organizational patterns at several hierarchical levels, so much more difficult to explore for free-living organisms. Furthermore, this hierarchical organization means that larger-scale processes may have a strong influence on local community structure (see Poulin 1998*a*; Poulin *et al.* 2000) and dynamics of parasites and microbes (see Grenfell and Harwood 1997; Rohani *et al.* 1999), indicating that these larger-scale phenomena cannot be ignored anymore. For instance, recent advances in epidemiology of childhood diseases have clearly shown the influence of spatial fluxes on local disease dynamics, recognizing structural similarities between the processes of metapopulation biology and infection dynamics (Grenfell and Harwood 1997; Rohani *et al.* 1999).

Price (1990) in his contribution to the seminal book by Esch, Bush, and Aho (1990) argued that parasite community ecologists should take a leading role in advancing areas of ecology with many parasite studies being attractive complements for investigating some of the major questions in population and community ecology. Nearly one decade and a half after, the intent of the present chapter is to synthesize the more recent developments in parasite and microbial community ecology, and to assess current perspectives regarding our knowledge of these communities.

To see where we are heading, consider a few simple questions one could ask about a parasite or microbial community. What determines the number of parasite species one host individual can harbour? Why are some parasite species extremely rare when others are very common? What is the local population abundance of a widely distributed macroparasite when compared to that of a rare species? These very basic questions of (parasite and infectious disease) community ecology have extraordinary little to do with small-scale processes, but on the contrary need that we explore larger-scale phenomena. Having described the different macroscopic patterns, we then explore the consequences of this research framework in population and community ecology of parasites and microbes. We opted in the present chapter to use examples from both the microbial and parasitological community literature to illustrate the various concepts. We conclude by highlighting what these findings mean for further study of population dynamics and community ecology of parasitic and infectious disease in wildlife and humans.

2.2 Parasite community organisation and species coexistence

2.2.1 The emergence of spatial ecology in infectious and parasitic diseases population and community dynamics

As for mainstream population and community ecology (see Putman 1994; Begon *et al.* 1996; Weiher and Keddy 1999), parasite population and community ecology has concentrated on local processes with an emphasis on local interactions between parasite species, and between these species and their host environment (see Kennedy 1975; Cheng 1986; Esch and Fernandez 1993; Combes 1995; Bush *et al.* 2001). Another aspect is the strong research effort made over the past decades on very untidy small-scale studies, which do not take a strongly quantitative approach to issues such as spatial patterns in species richness at very large scales or patterns in species distributions (but see Price 1980; Rohde 1982; Poulin *et al.* 2000; this chapter). For instance, what determines the structure of the local community of human infectious diseases in a given place of Western Africa has certainly as much to do with large-scale, biogeographical processes as it has to do with local conditions. This view is shared by an increasing number of researchers interested in the influence of climate variability on regional disease dispersion and diffusion, for instance (Dobson and Carper 1993; Rogers and Williams 1993; Hay *et al.* 1996; Patz *et al.* 1996; McMichael and Haines 1997; Rapport *et al.* 1998; Epstein 1999; Rogers and Randolph 2000; Aron and Patz 2001).

2.2.2 Some definitions and basic conceptual framework

Many processes studied by parasite and microbial community ecologists have clear linkages with larger-scale, regional phenomena, but since studies have focused too largely on small spatial scales they are obviously unable to put the communities into perspectives (see Lawton 2000; Poulin *et al.* 2000; this chapter). The assembly of parasites or microbial communities as for free-living ones is a multistage, multilayered process, and this forms a conceptually important framework on which to base further research investigations. First, it starts at the top of Fig. 2.1 with the largest-scale pool of species. The existence of a global-scale pool of parasite and microbe species is entirely relevant for many organisms like in the case of crop pests, viruses, bacteria, and fungi, or human infectious and parasitic diseases (see Rapport

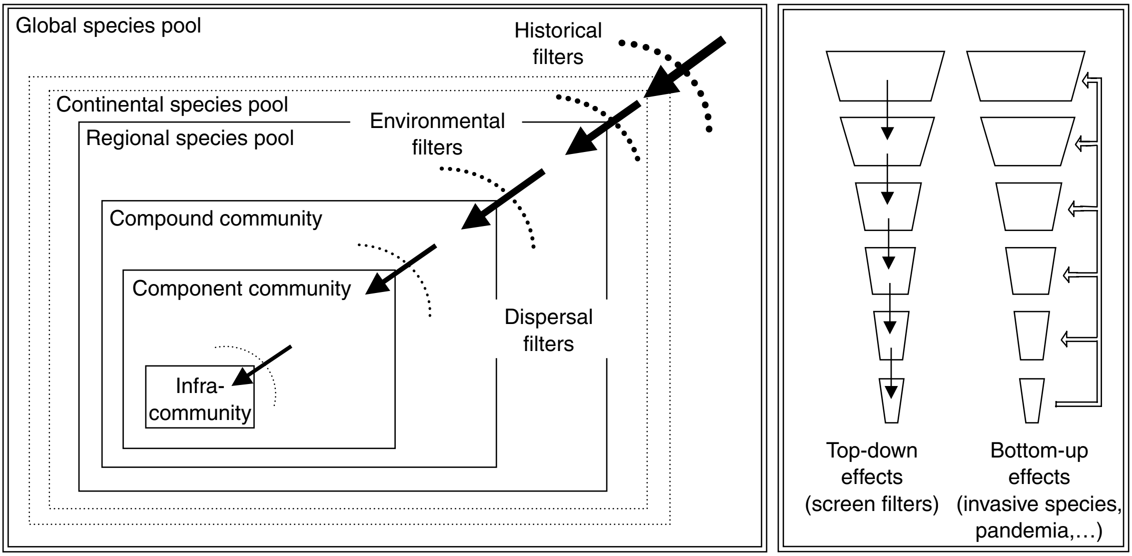

Figure 2.1 Schematic illustration of the main determinants of parasite or pathogen species richness in hosts. On the left: processes influencing species diversity are arranged into hierarchies in which different temporal and spatial factors may act. Any given level includes all lower levels, and it is included within all higher levels. On the right: the hierarchical scheme indicates that parasite or pathogen community assemblages at lower-spatial scales, for example an individual host, are strongly dependent on upper scales (top-down effect on community richness), but the opposite situation where lower-spatial scales may influence higher levels (bottom-up effect) is also possible.

Notes: Invasive species like crops or pandemia like HIV are illustrative of global impact of parasites and pathogens. Further research should reveal the respective roles played by 'top-down' and 'bottom-up' effects on community assemblages of parasites and microbes.

et al. 2002). This notion is at present made highly relevant by the development of transcontinental transports and economical exchanges between two distant biogeographical regions, making the Earth today a global village for many pathogens and diseases (see Poulin 2003*a*, and the later Section 2.3.2.4 'Latitudinal gradient in species richness'). The regional pool of parasite and microbe species, or metacommunity, is a more conventional and accepted notion in community ecology, and it exists within a biogeographic region like a continent or a subcontinent. Then, understanding the origin of the parasite or microbe pool requires a knowledge of the evolutionary history of host–parasite associations, of the geographic isolation of the continent, of the linkages between pathogens and the biological diversity present within the area, and so on (see Brooks and McLennan 1991; Combes 1995; Poulin 1998*a*). Local communities like those of macroparasites in fish populations or microbes in human populations assemble themselves from this regional pool through a series of filters (see Fig. 2.1). Differences in host population size and density or the spatial arrangement of host population habitat patches (high to low connectivity), for instance, may be responsible for the persistence or the extinction of parasite or pathogen populations moulding local communities (see Grenfell and Dobson 1995; Grenfell and Harwood 1997; Keeling and Grenfell 1997, 2002; Rohani *et al.* 1999). At the individual host level, infracommunities of parasites and pathogens again assemble themselves from the local pool of available species (see Fig. 2.1). If species can reach a host they may still find the environment unsuitable, species interactions may also operate or may be constitutive, and induced defences against invasion can intervene. Many processes described here have also clear parallels in within-host infection since each host individual is composed of many different sites more or less connected with one another, and available, or not, for parasite or pathogen establishment (see Holt 1999). This framework shows that different environmental filters work on all these communities representing important steps in community assembly and constitution (see Murray *et al.* 2002; Rapport *et al.* 2002).

Mainstream community ecologists have long debated on the important steps in community assembly working down from the larger scales largely dominated by regional, not local processes (see Ricklefs and Schluter 1993; Brown 1995; Rosenzweig 1995; Maurer 1999; Lawton 2000; Gaston and Blackburn 2000). This can be contrasted with a more traditional approach in both parasitology and epidemiology through the study of local phenomena for understanding the structure and dynamics of parasitic or microbe assemblages. However the 'top-down' and 'bottom-up' paths are clearly complementary, and the recognition of the importance of a regional or even global perspective in parasite and microbe population dynamics and community assembly theory would clearly benefit from more detailed attention than would be possible from either approach alone. Recent studies on the impacts of global environmental changes on disease population and communities dynamics (see Harvell *et al.* 1999, 2002; McMichael 2001; Martens and McMichael 2002) provide several good examples of how largest-scale studies are of particular relevance to both parasitology in wildlife and human epidemiology. It is also obvious that the 'context' of the beginning of an infectious disease outbreak transmitted from wildlife is clearly local (see for instance the cases of HIV), some having dramatically increased in incidence and expanded in geographic range panglobally (see Hahn *et al.* 2000; Daszak and Cunningham 2002).

As we know today from the study of complex hierarchical systems inspired by physics, both processes from the top to the bottom and from the bottom to the top of Fig. 2.1 (see also Allen and Hoekstra 1992; Allen *et al.* 1993) are certainly acting as forces controlling parasitic and infectious disease community assembly. Recognizing that often the determinants of both host animal (or plant) and individual human health may occur at levels higher within the ecosystem hierarchy is thus one of the major tasks of modern parasitology and epidemiology.

2.3 Emergent properties of parasite and infectious disease communities

2.3.1 On the search for regularities in parasite and infectious disease community structure and processes

One of the principal advantages of this two-way viewpoint of community assembly organisation is that it takes a sufficiently distant view of parasitological and epidemiological systems that the idiosyncratic details disappear, and only the important generalities remain (see Brown 1995; Rosenzweig 1995; Gaston and Blackburn 2000 for application in mainstream ecology; Poulin *et al.* 2000 and this volume for parasitological–epidemiological investigations). This may reveal general patterns, or regularities, that would otherwise have been entirely neglected (see Morand and Poulin 1998; Morand 2000; Morand and Guégan 2000*a*). Any scientific discipline must pass through a phase where the phenomena of interest are clearly and quantitatively identified (this chapter), and then the mechanisms underlying the observed patterns are explored and challenged with rigourous theoretical and empirical testing. Specifically, the recent developments in population dynamics of infectious diseases have clearly shown how useful generalizations, but not at the level of local human communities, might be indicative of significant regulation in spatial dynamics of those diseases (Ferguson *et al.* 2003). Nevertheless, the impossibility of using manipulative experiments in natural systems (case of wildlife diseases) and anthropogenic systems (case of epidemiology) means that it is often difficult to retain a single hypothesis among competing alternative solutions to understand the mechanisms that underlie the patterns (see Morand and Guégan 2000*a* for an illustration). Consequently, this inability to exploit manipulative experimentation over large-scales have forced parasitologists, plant-associated insect ecologists, and epidemiologists to use comparative approaches (see Aho and Bush 1993; Cornell 1993; Lawton *et al.* 1993; Poulin 1995*a*; Cornell and Karlson 1997; Morand and Poulin 1998; Choudhury and Dick 2000; Morand and Guégan 2000*a*; Guégan *et al.* 2001; Brändle and Brandl 2003; Nunn *et al.* 2003; Guernier *et al.* 2004) as macroecologists did before (Brown 1995; Rosenzweig 1995; Maurer 1999). The following sections attempt to illustrate this using different examples from the literature, and to discuss the consistency of the results with the various hypotheses used to explain the observed patterns in the light of recent advances in macroecology (see Gaston and Blackburn 2000), and comparative analysis in parasitology-epidemiology (see Poulin *et al.* 2000).

2.3.2 Parasite and infectious disease species richness

Undoubtedly, parasites and other kinds of microbes and associated organisms like phytophagous insects may represent more than half of the living organisms (Price 1980; de Meeüs *et al.* 1998; Morand 2000; Poulin and Morand 2000; Curtis *et al.* 2002; Brändle and Brandl 2001, 2003; Nee 2003), even if very few attempts have been made to rigorously quantify and delineate the differences in richness between free-living organisms on the one hand and their associated organisms on the other hand (but see Strong and Levin 1975; Strong *et al.* 1985; Hillebrand *et al.* 2001; Guernier *et al.* 2004 and hereafter). Most, if not all, organisms are hosts for parasites, comprising helminths, arthropods, fungi, or microbes, and if the pioneer work by Guernier and colleagues is representative of other (host) species, the overall biodiversity on Earth may be currently underestimated by more than an order of magnitude due to the unsuspected species diversity of parasites and other kinds of microorganisms (see Guernier *et al.* 2004 and hereafter). Investigations attempting to identify determinants of species richness of parasites and other kinds of associated organisms are now well represented in the recent parasitological literature (Poulin 1995*a*; Morand 2000; Poulin and Morand 2000; Brändle and Brandl 2001; Guernier *et al.* 2004) much more than a decade ago, and more research is needed on different symbiotic systems to examine the extent to which the observed patterns are supported or undermined. Here we draw attention to the four most popular and striking 'macroecological' patterns in the species richness of assemblages of parasitic and other kinds of associated organisms, and we promulgate how the search for consistency in common patterns, or not, from other symbiotic systems will contribute to the emergence of a more rigorous research agenda in parasitology and epidemiology.

2.3.2.1 Species–area relationship

The variation in species richness of parasites and other associated organisms is generally not random, but shows one regular pattern which is the species–area relationship (Simberloff and Moore

1997; Poulin 1998*a,b*; Morand 2000), a now-classical factor explaining the number of species likely to be found at any site in mainstream ecology (Brown 1995; Rosenzweig 1995; Gaston and Blackburn 2000). Usually, widespread hosts tend to have more parasite or infectious disease species than hosts with a more restricted geographical range because the increase of host range may allow the host to encounter more species (Gregory 1990). This pattern seems to hold both within host species (see Freeland 1979; Marcogliese and Cone 1991; Goüy de Bellocq *et al.* 2003; Calvete *et al.* 2004) and across host species (see Poulin 1998*a*; Morand 2000; Brändle and Brandl 2003 for a review). Alternatively, host body size may be taken to represent area size for parasites (see Guégan *et al.* 1992; Guégan and Hugueny 1994). Indeed, in interspecific comparisons among host species, many positive relationships have been reported between host body size and parasite species richness; however, the relationship is not universal, and there are many exceptions (see reviews in Poulin 1997; Morand 2000).

Still, the species–area relationship is generally a strong pattern in parasite diversity studies. For instance, the species–area relationship explains more than 50% of the total variation in species richness of phytophagous insects (Kennedy and Southwood 1984; Brändle and Brandl 2001), and around 14–30% of the variance in species richness of parasitic fungi (Strong and Levin 1975; Brändle and Brandl 2003). More interesting than the existence of a species–area relationship for symbiotic systems is what does this pattern mean? Or, put in other words, which processes may be responsible for the relationship?

One problem with this approach is that the search for correlates of species richness across populations of host species characterized by different geographical ranges (or size area for isolated systems) is often not independent of sampling effort (see Gregory 1990), and most studies have thus controlled for the effects of differential sampling of host species (Gregory 1990; Poulin 1998*a*). Whether it is correct still remains to be determined (Guégan and Kennedy 1996). Sampling effort may be strongly correlated with host geographical range and other biological factors which may covary with host range, for example, host size, host niche breadth, extinction/colonization, and temporal dynamics (see Gaston and Blackburn 2000), which then disappear after such a statistical control (see Guégan and Kennedy 1996).

The paper by Goüy de Bellocq *et al.* (2003) shows that the parasite species richness in the woodmouse, *Apodemus sylvaticus*, on western Mediterranean islands depends on the surface areas of the different surveyed localities (but see Dobson *et al.* 1992*a,b* for contradictory results). Other factors, that is, parasite species life-history traits and host species diversity, were also important as determinants of helminth richness and composition across isolated rodent populations. Fig. 2.2 illustrates the relationship between parasite species richness and surface area for the eight Mediterranean islands and three continental regions used in the study.

More interestingly, the authors demonstrate that the positive relationship observed between parasite species richness and surface area across woodmouse populations is not the result of a random process, but, on the contrary, it shows the existence of order, that is, nestedness (see corresponding Section, 2.3.2.4) in the presence/absence matrix of parasite species across different localities. Helminth parasites are organized according to a hierarchy of species, also called nested species pattern (see Guégan and Hugueny 1994), across surveyed areas: some parasite species are widespread across localities, and some others are

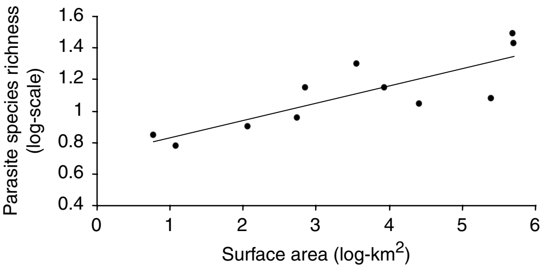

Figure 2.2 The relationship between log-species number and log-surface area for parasites of the woodmouse, *Apodemus sylvaticus*, on different islands and regions from Europe.

Notes: The line of best fit is a linear function of the form $y = 0.11x + 0.72$, $r^2 = 0.68$, $p = 0.0017$). The three points in the upper right side of the diagram are for Continental Europe, Spain, and Italy. Other points are for western Mediterranean islands, that is, Mallorca, Menorca, Formentera, Ibiza, Corsica, Port-Cros, Porquerolles, and Sicila.
Source: Redrawn from Goüy de Bellocq *et al.* (2003).

uncommon and found in only fewer areas (see Goüy de Bellocq *et al.* 2003). The richness and distribution of the different helminth species across areas depends not only on area size as previously shown but also on the type of parasite life cycle and host mammal species diversity. The explanations given by the authors are that larger areas may sustain larger host populations, an important parameter in epidemiology which determines the host resource needed for a parasitic or infectious disease agent to persist (see Grenfell and Harwood 1997; Keeling 1997), and thus may favor the existence of a higher parasite diversity (see Morand and Guégan 2000*b*). Then the difference observed in both the parasite species richness and composition across areas may be due to the fact that a parasite with a direct life cycle may have more chances to succeed in the colonization of a new host population compared with a parasite with an indirect life cycle which absolutely needs to find a suitable intermediate or definitive hosts to complete its cycle. Finally a locality with high host species diversity may be more favourable for parasitic or disease persistence, for example parasites with a complex life cycle finding more definitive host species to achieve their development.

A reconsideration of the study by Goüy de Bellocq *et al.* (2003) using Generalised Linear Models (see Wilson and Grenfell 1997; Venables and Ripley 1999) instead of simple regressions indicates that the data are strongly flawed by sampling bias, a fact that makes previous findings questionable. The new results (see Table 2.1) show that helminth component community richness variation across areas is strongly dependent on both sampling effort expressed as the host sample size per area (*F* value = 345.97, $p = 0.00034$) and the interaction between sampling effort and surface area (*F* value = 30.35, $p = 0.0118$), the largest areas being less sampled, on average, than smaller areas, with all other parameters kept constant in the model. Mammal host species diversity is then just marginally significant in the multivariate analysis (see Table 2.1). Surface area does not appear to be significant anymore. A stepwise elimination procedure using the Akaike criterion yielded similar results.

This new result indicates that sampling effort may exert strong bias in estimation of parasite species richness variation across different areas, notably in the case of the largest areas where rare parasite species may be missed during parasitological investigations. This point has been made before (Gregory 1990; Poulin 1998*b*), and sampling effort must be taken into account in any investigations of species–area relationships using parasite data. We also strongly recommend the use of multivariate analyses to take into account perverse effects exerted by sampling bias on statistics instead of *a priori* regressing species richness data against sampling and the use of residuals since sampling effort may also covary with other independent variables under study.

Table 2.1 Summary of Generalized Linear Model with a gaussian error structure for explaining the parasite species richness variation in woodmouse across 11 different areas

	Deviance	Resid. *df*	Resid. dev	*F* value	*p* (*F*)
Null	678.73				
Sampling size	538.77	9	139.96	345.97	0.00034
Host diversity	22.12	8	117.84	14.21	0.03269
Surface area	3.33	7	114.51	2.14	0.23978
Sampling × Host	6.33	6	108.18	4.06	0.13721
Sampling × Area	47.26	5	60.92	30.35	0.01178
Host × Area	40.53	4	20.39	26.02	0.01457
Sampling × Host ×Area	15.72	3	4.67	10.09	0.05021

Notes: Resid. *df* and Resid. dev are the residual degree of freedom and the residual deviance at each step of the procedure, respectively; *p(F)* is the probability statistics associated with the *F* test; Host diversity is the host mammal species diversity per unit area; Sampling × Host is the two-way interaction term between sample size and surface area, and so on (see text for explanation). The rank of introduction of terms in the successive models did not alter the main results as illustrated here.

2.3.2.2 *Species richness–isolation relationship*

More generally, species diversity is dependent on the fragmentation and isolation of habitats (Whittaker 1998). Fragmentation and isolation have promoted organism speciation and the build-up of endemic faunas on Earth (Brown 1995). Isolation and fragmentation are, of course, one part of the many factors promoting species diversity and composition (see Brown 1995; Rosenzweig 1995; Gaston and Blackburn 2000). Most organisms, including parasitic and infectious diseases in hosts (this chapter), exhibit patterns of similarity in composition and richness depending on geographic distance and isolation (see Poulin and Morand 1999; Morand and Guégan 2000*b*).

Perhaps one of the most important lesson to be learned from recent studies in host–parasite systems is the demonstration by Poulin and Morand (1999) that the geographical distance between component communities of parasites in freshwater fish is often the best, most general explanation of similarity in parasite species composition and to a lesser extent, of species richness across localities. Using multivariate analysis based on permutation methods (see Legendre *et al.* 1994), these authors conclude that patterns of parasite species composition across distinct isolated areas (i.e. distinct lakes in their study) strongly depend on the distances that separate the different localities, shorter geographical distances between isolated areas being associated with a greater similarity in parasite composition between them, and nearby lakes harbouring numbers of parasite species more similar than those of distant localities. Put in other words, there is in these parasitological data a tendency for species composition and richness to be autocorrelated over space. As mentioned by Poulin and Morand (1999), it might be more accurate to say that it is the isolation of a given locality within the network of patch areas that here matters instead of geographical distances among sites that roughly approximate this isolation. It is possible to have exceptions to this pattern, and many other factors may promote similarity between close localities in the composition and richness of parasite communities (see Kennedy *et al.* 1991; Hartvigsen and Kennedy 1993; Poulin 1998*a*). Nevertheless, the authors strongly suggest to consider the effect of geographical distance as a good index of isolation in further comparative analyses of parasite communities, and it should therefore become a basic requirement to control for the confounding and often important effect of geographical distance on the determinants of species composition and richness in parasite component communities.

Recently, Poulin (2003*b*) has shown that the influence of geographical distance on the similarity between parasite communities may follow a regular pattern. In the majority of parasite communities of fish and mammal hosts, the similarity in the species composition of communities decays exponentially with increasing geographical distance between localities (Poulin 2003*b*). Exponential rates of decay in similarity have also been reported for plant communities (Nekola and White 1999), and further emphasize the importance of geographical isolation.

One illustrative example of the effect of geographical distance and isolation on parasitic and infectious disease communities is that of oceanic islands. Typically islands have fewer species per unit area than the mainland, and this distinction is more marked the smaller the island and the farthest it is from a continental source (Rosenzweig 1995; Whittaker 1998). Very few studies have investigated parasite species community richness and composition on islands (see Kennedy 1978; Mas-Coma and Feliu 1984; Kennedy *et al*. 1986*a*; Dobson 1988*a*; Dobson *et al.* 1992*a*; Miquel *et al.* 1996; Goüy de Bellocq *et al.* 2002, 2003). The main conclusions reached by Dobson *et al.* (1992*a*) concerning parasite species richness and composition in *Anolis* lizards from northern Lesser Antilles islands are that they show a relatively depauperate parasite community when compared with lizards sampled on the larger Carribean islands, for example, Cuba, or on continental areas, and that these differences are associated with the life history attributes of the different parasite species in the assemblages. On the whole, Goüy de Bellocq *et al.* (2003) reach the same conclusions (see above), but they were unable to more formally characterize an effect of geographical distance and isolation in-between Mediterranean islands on parasite species richness and composition in the woodmouse. Examples of studies of pathogen communities and species composition in animals and humans on islands are even more scarce. Collares-Pereira *et al.* (1997) provide the first epidemiological data on pathogenic leptospires serovars diversity in insectivore and rodent species in the Azores archipelago, and they conclude to a low serovars diversity of three within this group of islands out of a total of nineteen serogroups more largely represented over the world. Surprisingly, there are only few studies that have quantified pathogen species richness and composition on islands for human communities in a way similar to what is traditionally done in community ecology. Based on unpublished data from one of us

(Guégan and Guernier, unpubl. data), we show here that on a total set of 197 different countries all over the world, the species richness of pathogens including viruses, bacteria, fungi, protozoa, and helminths is lowest on the 73 islands compared with the mainland countries (see, Table 2.2). Even after controlling for confounding effects that may be exerted by factors like the socio-economical power, the population size in number of inhabitants or the latitudinal position of the country, the island factor still explains 24.1% of the total variation in pathogen species diversity across areas. This result on pathogen species assemblages in humans is indicative that isolation and/or distance from a continent may be highly responsible for lower species richness in those localities. As suggested by the work of Goüy de Bellocq *et al.* (2003), islands sample only from the dispersive portion of the mainland pool. This effect must, of course, be distinguished from area size since the human pathogen study (see Table 2.2) has kept its effect constant in a multivariate analysis. Present-day distances between isolated islands and a regional biogeographic pool, even if they do not strictly reflect distances at the time of disease colonization, may however provide a rough index of isolation.

Table 2.2 Summary of Generalized Linear Model with a poissonian error structure and a log-link for explaining the species richness variation in human infectious diseases across a set of 197 different continental (124) or isolated (73) countries

	Deviance	Resid. *df*	Resid. dev	$p\ (\chi^2)$
Null	265.56			
Island	64.07	196	201.49	0.00000
GNP	2.63	195	198.86	0.10466
Population size	40.32	194	158.54	0.00000
Surface area	19.60	193	138.94	0.00001
Latitude	8.80	192	130.14	0.00301
Island × Surface area	2.98	191	127.16	0.08404

Notes: Dispersion parameter in the model is 0.67. Island is coded 1 and continental area is coded 0; GNP is the Gross National Product per country (in US $) to control for its effect on final statistics; Population size is the number of inhabitants; Latitude is the geographical position of each country in degrees and minutes; see also Table 2.1; $p\ (\chi^2)$ is the probability statistics associated to χ^2 test. Models were built with independent variables and their two-way and three-way interaction terms. The rank of introduction of terms in the successive models did not alter the main results as illustrated here.

From the present human diseases data set, information concerning the Caribbean islands and the surrounding continental countries from Northern, Central, and Latin America representing the mainland, it is informative to see that remote islands from the Gulf of Mexico are poorest in pathogen species when compared to what is observed on the continent and even on close islands like Trinidad & Tobago, for instance (see Fig. 2.3). When considering the confounding effects exerted by covariate factors (notably the economic power of a nation) on disease species richness across localities, the influence of distance still remains (statistical data not illustrated): distance from a continental regional pool (49.1% of the total variation explained; $p = 0.00001$), the total area size of islands (28.9% of the total variation explained, $p = 0.00001$), and to a lesser extent human community size (5.9% of the total variation explained, $p = 0.028$) are the best predictors of pathogen species richness in human populations among the nineteen Caribbean islands and the fifteen surrounding continental countries. These findings based on a study of community assemblage of human diseases are in accordance with studies on population dynamics of infectious diseases on islands (see Black 1966). According to

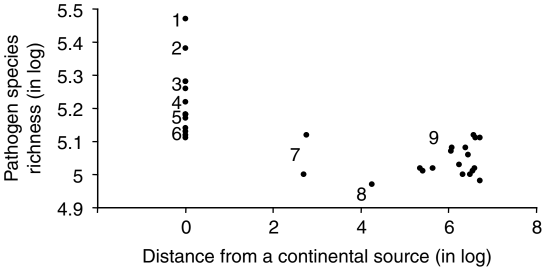

Figure 2.3 The relationship between log-species number and log-distance (in km^2) from the continent for human infectious diseases in different Caribbean islands ($n = 19$) and surrounding continental countries ($n = 15$) from Americas.

Notes: Codes are 1 : USA; 2 : Brazil; 3 : Venezuela and Mexico; 4 : Colombia and Panama; 5 : Surinam, Guyana, Honduras, Guatemala, and Costa Rica; 6 : French Guiana, San Salvador, Trinidad & Tobago, Puerto Rico, Nicaragua, Haiti, Dominican Republic, Belize; 7 : Guadeloupe, Cuba, Martinique, Jamaïque; 8 : Dutch Antilla, 9 : Aruba, Caïman Islands, Montserrat, Grenada, St Kitts & Neville, Antigua & Barbuda, Barbados, St Vincent and Dominica.

Price (1990), as local host abundance increases, so the effective population size for maintaining parasite populations increases, resulting in more parasite species being maintained in larger communities. Thus species dynamics of infectious diseases might be in many ways analogous to population dynamics (e.g. critical community size threshold), (see Grenfell and Harwood 1997; Keeling 1997; Broutin *et al.* 2004). There are obviously similarities between species and population maintenance and dynamics (see Brown 1995), and all these points need to be developed in further research on infectious diseases in wildlife and humans as we learn more about the patterns of variation in infectious disease species richness with respect to island size, isolation, and host community size. The above findings do not stipulate that modern events, and more particularly transcontinental exchanges, do not influence infectious disease dispersal and maintenance in heterogeneous environments, but they strongly suggest that we need to explore the impact of spatial heterogeneity on the course of infectious disease species dynamics, and the importance of these variables, for example, area size, isolation, community size, to better grasp the abundance, distribution, and identity of pathogen species within local habitats.

A major outcome of fauna (or flora) isolation is endemism; thus old and/or remote islands tend to generally have a large degree of endemism (see Whittaker 1998). The term endemism refers to the restricted ranges of taxa in biogeography, and it is used differently in epidemiology–parasitology. We refer here to the former definition. Little is known about parasite or infectious disease community assemblages in endemic hosts, and Morand and Guégan (2000*b*) have concluded with some predictions based on both empirical studies and mathematical modelling that hot spots of (host) endemism are also the foci for a large diversity of endemic parasites and pathogens, and that restricted areas and/or low host community sizes are associated with a decrease in parasite or pathogen species numbers (see above). Regarding the existence of endemic parasites or pathogens, we can only speculate on their existence on Earth, and they are probably legions. Many parasitological investigations have focused their efforts on the impacts of exotic pathogens and pests on native host species, but an important advance in future research should be the recognition of endemic parasites and pathogens, and the role they may play in maintaining and regulating biodiversity and ecosystem dynamics. Recent research on emergent pathogens might shed light on their importance in nature (see Aguirre *et al.* 2002).

2.3.2.3 Local–regional richness relationship

Much parasitological literature on species diversity patterns has been devoted to local mechanisms whereas in recent years large-scale processes have been regarded as important determinants of the species richness of local communities in free-living organisms (see Lawton 1999; Gaston and Blackburn 2000). Implicit in many ecological studies is the important recognition that regional and historical processes may profoundly affect local community structure (Brown 1995; Rosenzweig 1995; Lawton 1999, 2000). Questions of spatial scale have been addressed only very recently in parasite community ecology (Price 1980; Aho 1990; Aho and Bush 1993; Kennedy and Bush 1994; Kennedy and Guégan 1994; Barker *et al.* 1996) probably because traditional parasitology has been too medically orientated over a long time with a major focus on very fine-scale studies.

Simply because every parasitic, parasitoid, or even microbe species cannot be present everywhere, we do not expect every species occurring within the regional pool to affect the composition of every local community. A central method used for the recognition of the importance of regional and local processes is the regression of regional species richness against local species richness plots (see Lawton 1999; Srivastava 1999; Hillebrand and Blenckner 2002), and several contributions have tried to disentangle the regional and local constraints in free-living communities (see Srivastava 1999; Shurin and Allen 2001; Hillebrand and Blenckner 2002, for recent reviews). The test requires estimates of species richness for a given group of organisms at both local and regional spatial scales and a statistical evaluation of their relationship. When local richness is regressed against regional richness and the relationship is linear, the communities are

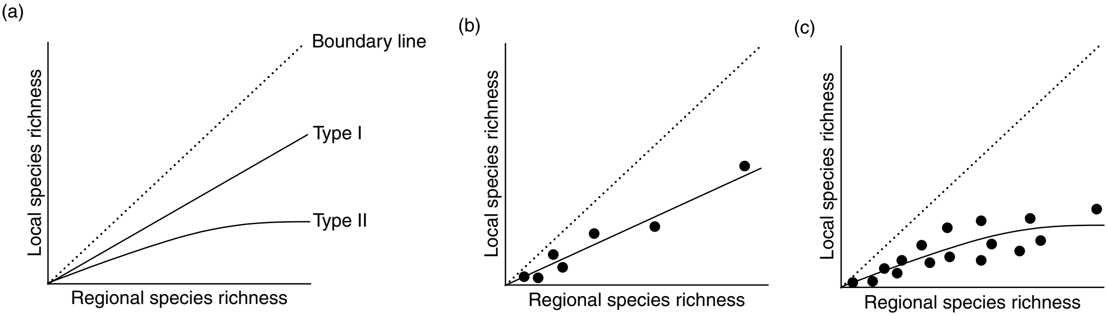

Figure 2.4 The relationship between regional and local species richness for parasite, pest and pathogen organisms. (a) Because of the hierarchical processes illustrated on Fig. 2.1, every parasite, pest or pathogen species present within the regional pool is unlikely to occur everywhere, which thus determines a boundary line never reached for which *y* equals *x*. Local species richness both at the infracommunity and component community scales are usually less than regional richness, and two kinds of relationships may then exist. A type I curve indicates proportional sampling in which local species richness increases linearly with regional richness. A type II curve saturates with local species richness above a threshold for higher regional richness. In nature, parasite, pest or pathogen community assemblages lie anywhere between type I and type II systems (see Cornell and Karlson 1997). (b) Example where the richest regional (component) communities are associated with the richest infracommunities and vice versa, suggestive of no saturation in parasite species. Helminth parasites of introduced freshwater fish in the British isles (Guégan and Kennedy 1993) or of natural populations of partridges in Spain (Calvete *et al.* 2003) are clear examples of unsaturated systems. (c) Examples where local species richness may be fixed by internal constraints indicative of saturation in local species communities. Intestinal helminth infracommunities (see Aho 1990; Kennedy and Guégan 1994; Calvete *et al.* 2004) generally are examples where saturation in parasite species may occur (see also text for contradictory results).

unsaturated and are said to exhibit 'proportional sampling' of the regional species pools. If the relationship is a somewhat curvilinear function, the possibility of saturation may then arise (see Fig. 2.4). Although this type of analysis appears to be straightforward, several pitfalls have been discussed elsewhere (see Creswell *et al.* 1995; Srivastava 1999; Shurin *et al.* 2000). A major question is the definition of what exactly regional and local richnesses mean for parasite communities, and the way their measurements are best comprehended (Kennedy and Guégan 1994; Barker *et al.* 1996). Usually, regional (Kennedy and Guégan 1994) or continental (Aho and Bush 1993) parasite species richnesses, that is to say spatial scales reflecting a naturally occurring hierarchy from which local parasite communities may be drawn, have been used to represent regional pools. Morand *et al.* (1999) used another estimate of regional species richness defined as the component community richness, but the authors were faced to the problem of defining exactly the spatial hierarchy at which processes may operate in open marine systems. The measure of local parasite species richness adopted sometimes is the mean or maximum number of parasite species in the parasite component communities known to the authors (see Aho and Bush 1993; Kennedy and Guégan 1994), but a more correct definition of local species richness seems to be the mean (Kennedy and Guégan 1994; Morand *et al.* 1999) or even maximum (Poulin 1996*a*, 1997; Calvete *et al.*, 2004) infracommunity parasite species richness.

Generally, all the studies agree on an important influence of both regional and local factors, but their relative importance may differ between categories of organisms. Concerning parasite, parasitoid, and microbe species communities, the diversity of species in local (at the host population level) assemblages is intuitively regulated both by local (e.g. interspecific competition, habitat heterogeneity) and by regional factors (e.g. evolution, migration, history). The studies published so far on free-living organisms have stressed the prevalence of type I communities (see Fig. 2.4) interpreted as an indication of unsaturation of local assemblages with generally weak or no effects of local interactions on species richness. Analyses of local to regional species richness performed on host-associated organisms like parasites or parasitoids (Cornell 1985; Aho 1990; Bush 1990; Hawkins and Compton 1992; Aho and Bush 1993; Lawton *et al.* 1993; Dawah *et al.* 1995; Kennedy and Guégan 1994, 1996; Poulin 1996*a*, 1997; Morand *et al.* 1999; Frenzel and Brandl 2000; Calvete *et al.* 2004) have, on the contrary, shown the existence of both type I and II communities (see Fig. 2.4). Particularly, the commonness of type II communities in host–parasite systems, and more specifically for helminths, may be illustrative of limiting factors shaping these local communities. In addition to the occurrence of saturated assemblages shown in parasite systems compared to other organisms, the three clearest results that emerge from the published parasitological literature available today may be summarized as follows.

First, most studies on herbivorous insects (see Dawah *et al.* 1995; Frenzel and Brandl 2000) and fish ectoparasites, that is, helminths and copepods (see Morand *et al.* 1999), have identified that empty niches are common and that local communities are unsaturated. As such, many natural enemy communities are subject to strong regional influences then providing opportunities for new invasive species to become established. The opposite can be observed for many studies on internal parasites like intestinal helminths of fish (Kennedy and Guégan 1994), of amphibians and reptiles (Aho 1990), and of birds (Bush 1990; Calvete *et al.* 2004) where local forces may contribute to parasite community structure. Poulin (1996*a*, 1997) showed, on the contrary, that for 31 intestinal helminth communities in bird hosts and 37 in mammal hosts the relationship between the maximum infracommunity richness and component community species richness was linear, indicating the absence of species saturation and the availability of vacant niches in organisms accepted to generally have species-rich helminth communities (see Bush and Holmes 1986*a,b*; Stock and Holmes 1988). The contrasting results may in part be due to the fact that Poulin's (1996*a*, 1997) analysis included different host species, whereas many of the studies that found a curvilinear relationship between infracommunity richness and component community richness included only different host populations of the same host species (e.g. Kennedy and Guégan 1996; Calvete *et al.* 2004).

Then, second, the only intestinal helminth communities which exhibit unsaturated assemblages are those occurring in introduced fish species in the British Isles, that consist of non native fishes not having had enough time to accumulate sufficient helminth species from the native pool (Guégan and Kennedy 1993) to develop ecologically interactive communities (Kennedy and Guégan 1994). A recent study by Torchin *et al.* (2003) which compared the parasite species richness between introduced and native populations for 26 host species of molluscs, crustaceans, fishes, birds, mammals, amphibians, and reptiles also confirmed the reduced parasitization of introduced organisms suggestive of an absence of saturation in those parasite communities (see Figs. 2(c) and (d) in Torchin *et al*. 2003).

Third, major advances in our understanding of saturation versus non saturation of local parasite communities have been made in recent years. Cornell and Karlson (1997) and Srivastava (1999) drew attention to the necessity of the demonstration of other lines of evidences of niche and habitat relationships combined with information on local versus regional relationships. In particular, Rohde (1998) using randomization procedures highlighted the many scenarios in which a curvilinear local to regional relationship might be generated without requiring the necessity of species saturation. Using a comprehensive survey of marine fish ectoparasite communities, Morand *et al.* (1999) examined the effects of interspecific aggregation on the level of intraspecific aggregation in infracommunities, and they demonstrated that interspecific interactions were reduced relative to intraspecific interactions thus facilitating species coexistence in rich communities (see Tokeshi 1999 for further details on species coexistence). This pattern was highly coincidental with a positive linear relationship between infracommunity species richness and total parasite species richness obtained after controlling for the confounding effect exerted by phylogeny, indicative of no saturation in ectoparasite communities of marine fish (see Rohde 1991, 1998). In a recent study, Calvete *et al.* (2004) showed the existence of a curvilinear relationship between local and regional species richnesses of intestinal helminth infracommunities for eight populations of the red-legged partridge in Spain, even after checking for the confounding effect of geographical distance among localities on species richness calculations. Interestingly, this finding was confirmed by a demonstration of negative interspecific associations for the helminth species community, especially between cestodes and other helminths parasitizing the bird intestines.

All these results illustrate a number of important issues about the understanding of local–regional richness relationships in parasite or microbe community assemblages. First, demonstrating the effects of saturation, or not, in infracommunity assemblages requires that we simultaneously use additional investigations of interspecific interactions, or that published examples of the types of interactions exist, to test for the possible existence of interspecific competition. Neither of the two patterns for community assemblage organization, that is, the local to regional richness relationship and the demonstration of interspecific competition, is conclusive on its own. Interestingly, conclusions about the degree of concordance in the saturation of local communities, or not, between two or more methods may yield generality, but most of studies to date have only considered one option to test for the shape of interspecific relationships (but see Calvete *et al.* 2004). Second, the study of interspecific competition in local communities of parasites and pathogens has shaped the development of our understanding of species interactions, that is, importance of local processes. Thus, consideration of local to regional richness relationships in parasite or pathogen communities should lead to more attention being paid to the importance of large-scale patterns in parasitology and epidemiology. Third, one area in which the combination of these two methods should be fruitful is in the connection that might exist with the density of parasites or microbes. Indeed, if competition is important within parasite or microbe communities, one would expect to see density compensation in those communities with few species. If complete compensation occurs, there should be no relation between parasite density or biomass and local species richness, while if there was no density compensation a linear trend would thus be expected (see Oberdorff *et al.* 1998; Griffiths 1999 for taxonomic groups others than parasites). Furthermore, the linkages between interspecific competition, (un)saturation and density compensation in parasite or microorganism community assemblages will require more research from community ecologists, parasitologists and epidemiologists. Notably, these issues should be highly relevant in the field of veterinary and medical sciences since any alteration of local habitats (from the point of view of one parasite species, for example, one intestine) and other disturbances exerted by humans (e.g. the use of drugs like helminthicides or antibiotics) should reduce parasite or pathogen populations from time to time, making ways for more resistant species or aliens to increase or to invade. The idea of saturation predicts that an invasive species (like a crop or an emerging virus) should not invade an infracommunity in individual hosts, or should do so only with the consequence of excluding a resident member species, that is, density compensation by new individual invaders. The study of interconnectedness between these patterns and our efforts at understanding the processes behind will require judicious choices of both host and parasite or pathogen taxa, and at different levels of spatio-temporal organization. As discussed before, patterns of within-host microbial species richness will also likely profit from a greater consideration of dynamical processes in patchy and discontinuously distributed environments, microbial persistence, and abundance in a particular tissue-habitat being influenced in several ways by biogeographical-like processes within host individuals.

2.3.2.4 *Latitudinal gradient in species richness*

Latitudinal gradients in species richness of free-living organisms are one of the most consistent large-scale trends that we can observe in nature, and one of the best documented patterns in the ecological literature (see Hawkins *et al.* 2003 for a recent review), but there are still exceptions (Brown 1995; Rosenzweig 1995; Gaston and Blackburn 2000). This pattern does hold not only for the hosts as a whole, but also for some parasitic and infectious disease organisms (Rohde 1992; Poulin and Rohde 1997; Rohde and Heap 1998; Calvete *et al.* 2003; Guernier *et al.* 2004; but see Poulin 2001; Poulin and Mouritsen 2003), which means that it could be a simple consequence of the observed latitudinal cline in host species diversity. Parasitological or epidemiological investigations on large spatial scales are rare, and there is undoubtedly a need for more comparative studies. Expectations of rich low-latitude parasite communities have been suggested by some authors (Kennedy 1995; Salgado-Maldonado and Kennedy 1997) while it is intuitive from other studies (Poulin and Guégan 2000; Guégan *et al.* 2001) that a latitudinal richness gradient exists for fish ectoparasite and human infectious disease communities, respectively.

Across 80 localities from 16 Spanish provinces, there is a marked cline in helminth species richness and composition in the red-legged partridge (*Alectoris rufa* L.) (Calvete *et al.* 2003). The highest levels of helminth richness are encountered in southern provinces of Spain (e.g. Badajoz, Huelva) and the lowest in northern ones (e.g. Alava Burgos Santander, Alava Navarra) (Calvete *et al.* 2003). Statistical analyses controlled for the effect of host age, sex, body condition, and time at which the study was carried out, and thus it is unlikely that these variables contributed to the spatial variation in helminth distribution and species richness across the study area. The cline in parasite species richness and composition across Spain was mirrored by the measures obtained for both infra- and component communities levels, indicating that the poorest component communities in the north correlated well with the poorest infracommunities. In the north, parasite communities were characterized by having one, that is, *Dicrocoelium* sp., or a few dominant widespread species. In contrast, in southern provinces, helminth communities were more species-rich with several codominant helminth species, *Raillietina tetragona*, *Subulura suctoria*, *Cheilospirura gruweli* (see Calvete *et al.* 2003 for further details). The answer to why there are more helminth species in the red-legged partridge in southern Spanish provinces than in the north is that the pattern may be related to variation in definitive host densities and to the distribution and diversity of intermediate hosts. According to Calvete *et al.* (2003), red-legged partridge populations are usually denser in the centre and south of Spain which represent the core-area of their range. This finding would tend to suggest that high densities of definitive hosts might be associated with a greater abundance of helminths and greater helminth species richness as a whole. In addition, and this second hypothesis is not mutually exclusive of the definitive-host density hypothesis, a greater abundance or diversity of arthropod intermediate hosts in the centre and south of Spain might result in the exposure of partridges to a wider variety of potential parasite species (see Poulin 1995*a*). Calvete *et al.* (2003) argued, based on correlation statistics using factorial scores from multivariate analysis, that the north–south abundance and richness variation of helminths in partridges might be to a large extent determined by higher temperature in southern regions of Spain, environmental conditions causing an increase in the survival or activity of intermediate forms of parasites with life-history stages outside their definitive hosts. These results suggest that variation in the distribution of helminths in partridge hosts are probably associated with variations in the distribution of their definitive and intermediate hosts and the local ecological conditions that may act on these host–parasite relationships.

One recent study (see Guernier *et al.* 2004) goes one step further in the explanation of the existence of a latitudinal gradient of species richness for pathogen species in human populations. Compiling data on parasitic and infectious diseases for a total set of 229 different species of pathogens in human hosts, including bacteria, viruses, fungi, protozoa, and helminths, Guernier and colleagues (2004) showed that after correcting for cofactors, that is, area, socio-demographic variables, physical and environmental parameters, that could exert a strong influence on the relationship between latitude and parasitic and infectious diseases species richness, one still observes that the species richness in human pathogens is strongly correlated with latitude (Fig. 2.5) with, on average, tropical areas harbouring a higher pathogen diversity than more temperate areas. This new result shows that pathogen species richness is not distributed homogeneously across the planet but there is a marked cline with the highest levels of parasitic and infectious diseases species diversity near the Equator, and the lowest in northern areas. The cline in pathogen species richness occurs for the vast majority of groups of pathogens the authors analysed (7 times out of 10, exceptions being bacteria, viruses with direct transmission, and fungi). Interestingly, this similarity between many free-living organisms and pathogens is useful, because several common extrinsic and/or intrinsic factors might cause these common sets of pattern. Other variables are indeed

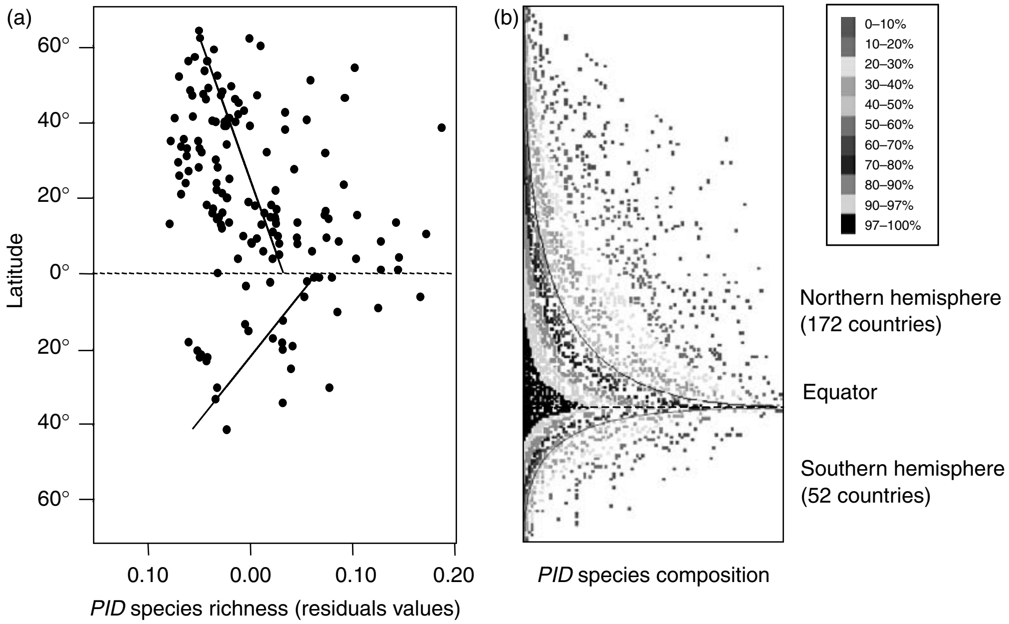

Figure 2.5 (a) Relationship between parasitic and infectious disease species richness and latitude in human populations across the two hemispheres. Linear relationships between species richness and latitude (dotted lines) are highly significant ($F = 12.29$, $df = 29$, $p = 0.0015$ and $F = 18.01$, $df = 130$, $p < 0.0001$ for Southern and Northern hemispheres, respectively). Residuals of species richness on the x-axis were extracted from minimal GLIM models controlling for the effects of confounding factors on disease species diversity estimates. Latitudes are expressed in degrees. (b) Presence/absence matrix for the 229 distinct parasitic and infectious disease species across the two hemispheres. The spatial distribution of pathogen species were organized according to the procedure adopted by the *'Nestedness Temperature Calculator'* (see Atmar and Patterson 1995). One hundred and seven ubiquitous pathogen species where eliminated from the entire data base since information they contained where entirely redundant with the most ubiquitous species already present into the matrix. Figure 2.5 (b) was generated after 1000 randomized permutations. This distribution is nonsymmetrical because of the 224 studied countries, 172 countries are found in the Northern hemisphere versus only 52 in the Southern one. Figure 2.5 (b) indicates that species diversity decreases as we move northwards or southwards from the equator ($F = 28.2307$, $df = 161$, $p < 0.001$). The occurrence boundary lines (black exponential curves) were fitted by non-linear regression ($y = 1.51 + 20.01e^{-0.29x}$ and $y = 1.65 + 35.87e^{-0.36x}$ for Northern and Southern hemispheres, respectively). See Guernier *et al.* (2004) for further details.

Source: Courtesy by *PloS* (Biology).

important in explaining global-scale patterns of human pathogens (e.g. modernization, urbanization, or impoverishment, especially in developing countries), but the fact that the authors considered such effects in their multivariate analyses tends to indicate that biogeographical forces are also important indeed in shaping the distribution and abundance of pathogen species. These results thus challenge the conventional wisdom that socioeconomic conditions are of preponderant importance in controlling or eradicating diseases.

Over the last three decades, the number of hypotheses advanced to explain the latitudinal gradient has increased from six (Pianka 1966) to nearly thirty, proffered by Rohde (1992). Some of these include spatial heterogeneity and patchiness, competition, predation, parasitism, mutualism, area, environmental stability, productivity, seasonality, solar energy (see Rohde 1992 for a general description). In reality, several factors may be acting in concert or in series, and among the numerous explanations given it is possible to substantially narrow the list of the most plausible explanations since many factors may be entirely redundant or untestable (Hawkins *et al*. 2003). For instance, Gaston and Blackburn (2000) listed only three plausible explanations for latitudinal richness gradients: area, energy, and time. They discarded the possibility that random location of species might be responsible for the latitudinal species gradient based on the absence of formal evidence. Area has often been cited as a simple hypothesis (see section on species–area relationships) to explain that the tropics, which really harbour the highest richness for many groups of organisms, also have the largest terrestrial surface area, that is, the geographical area hypothesis (see Rosenzweig 1995). This explanation may not be plausible when considering the latitudinal gradient of pathogen species in human populations as observed by Guernier and colleagues since both the surface area and continental mass effects have been taken into account in multivariate analysis.

Furthermore, and probably more important than the existence of a latitudinal gradient in species richness is the demonstration of an overall pattern of spatial distribution of parasitic and infectious diseases species in human populations on Earth that conforms to a nested species subset hierarchy (see Guégan and Hugueny 1994; Guégan *et al.* 2001; Guernier *et al.* 2004). Nestedness structure indicates that species (here pathogens) that compose a depauperate community (here temperate conditions) statistically constitute a proper subset of those occurring in richer communities (here warmer conditions in tropical areas), but the converse situation, that is, pathogen species solely occurring in depauperate communities but not in the richest ones, is either not found or not properly substantiated. This pattern, although not considered in the ecological literature (but see Gaston and Blackburn 2000 who suspected the existence of a connection between the two patterns; see later), was strongly associated with latitude, indicating that the progression of pathogen species richness is from species-poor countries in more temperate areas to species-rich ones when reaching tropical zones (see Fig. 2.5).

Using Monte-Carlo simulations (see Manly 1991; Guégan and Hugueny 1994) to test the hypothesis of parasitic and infectious diseases spatial organisation on the largest scale, Guernier *et al.* (2004) assessed the degree of nestedness of the system using two different but complementary programmes: (*i*) 'Nestedness' (Guégan and Hugueny 1994) and (*ii*) 'Nestedness Temperature Calculator' (Atmar and Patterson 1995). In the former programme, pathogen species were either selected with uniform probability (R_0) or with a probability proportional to their incidence (R_1) (Guégan and Hugueny 1994) whereas in the latter one only a R_{00} procedure was retained (Atmar and Patterson 1995); (see also Wright *et al*, 1998; Cook and Quinn 1998; Gaston and Blackburn 2000 for further details). Results from Monte Carlo simulations showed that the global distribution of human pathogens was strongly nested ($N_s = 2481.4$, R_0 and R_1 procedures, $p < 0.0001$), with some slight differences that were found across the different groups of aetiological agents (all groups, $p < 0.0001$, but except for vector-borne viruses, with the R_1 procedure ($N_s = 1787$, $p = 0.0015$). When considering the Northern and Southern hemispheres separately, both were highly nested (R_0 and R_1

procedures, $N_s = 6602$, $p < 0.0001$ and $N_s = 1230$, $p < 0.0001$, respectively). This was confirmed by the R_{00} procedure used by the 'Nestedness Temperature Calculator' program (Atmar and Patterson 1995), which provides a useful graphic representation of the results (Fig. 2.5), showing that parasitic and infectious diseases species diversity decreases as we move northwards or southwards from the equator ($F = 28.2307$, $df = 161$, $p < 0.001$), (see Guernier *et al.* 2004). Results from all three nestedness models (see Wright *et al.* 1998) explained reasonable amounts of the nested pattern in human pathogen species across latitudes.

Wright *et al.* (1998) have suggested a cogent explanation for nestedness as a series of probabilistic filters, screening species with particular characteristics: local habitat suitabilities, differential colonization capacities of species, and sustainability of viable populations within their environment. Additionally, as pointed out by Gaston and Blackburn (2000), nestedness might be an inevitable second-order consequence of the same factors that cause variation in species richness and range size along latitudinal gradients. It is exactly the view with which Guernier *et al.* (2004) totally agree with the example of pathogen species diversity in human on a broad-scale.

Searching for the common causes explaining the existence of both patterns, *i.e.* gradient in species richness and nested structure, for parasitic and infectious diseases diversity and composition in human communities, Guernier *et al.* (2004) retained the energy hypothesis as a likely candidate for explanation. The energy hypothesis is a climate-based hypothesis that claims that energy availability generates and maintains species richness gradients (see Hawkins *et al*. 2003 for a recent review). Many studies have successfully correlated gradients in species diversity with variation in the climatic environment, a relationship thought to shape large-scale biogeographic patterns (Hill *et al.* 1999). The authors decomposed the potential effect of climate on pathogen diversity into Pearson's correlations to more deeply analyse the kinds of relationships between each of the four climatic variables and disease richness under study. The results show significant positive correlations between pathogen species richness and the maximum range of precipitation after Bonferonni multiple correction for all six of the parasite or infectious disease taxa considered: bacteria ($r = 0.3545$, $df = 213$, $p < 0.0001$), viruses directly transmitted from person-to-person ($r = 0.2350$, $df = 215$, $p < 0.0001$), viruses indirectly transmitted via a vector ($r = 0.3575$, $df = 215$, $p < 0.0001$), fungi ($r = 0.3554$, $df = 216$, $p < 0.0001$), protozoa ($r = 0.3744$, $df = 216$, $p < 0.0001$), and helminths ($r = 0.4270$, $df = 215$, $p < 0.0001$). On the other hand, the relationship between pathogen species richness and monthly temperature range was only significant for three groups of pathogens: bacteria ($r = 0.3016$, $df = 213$, $p < 0.0001$), viruses directly transmitted ($r = 0.2142$, $df = 214$, $p = 0.0015$), and helminths ($r = 0.2590$, $df = 213$, $p = 0.0001$). No relationship between parasite species richness and mean annual temperature appeared to be significant after Bonferroni corrections. Finally, only the relationship between bacterial species richness and mean annual precipitation was significant ($r = -0.1987$, $df = 213$, $p = 0.0034$). No or very slight differences between total and categories of pathogen species richnesses and some climatic factors were observed between Northern and Southern hemispheres.

Many factors are involved in the determination of the climate in an area, particularly latitude, altitude, and the position of the area relative to oceans and land masses. In turn, the climate largely determines the species of plants and animals that live in those areas. According to the results of Guernier *et al.* (2004), the maximum range of precipitation is highly correlated with latitudinal gradient of pathogen species, the parasitic species diversity significantly increasing with this climate-based factor. Interestingly, the variation of precipitation around the mean was overall a better predictor of pathogen species distribution than its average value, thus indicating that pathogen species, their vector and host populations might best function over only a wide range of precipitation, which is actually found in many tropical regions of the world, those regions having more or less distinct wet and dry seasons during the year. Many parasites obviously require water as the basic medium of their existence, and many others strongly need wet conditions to complete their life cycle, for example vector-borne diseases. Often, many microorganisms are also constrained by the humidity of the atmosphere. Undoubtedly, the physical factor of precipitation variation may affect parasitic and infectious microorganisms, vectors and/or hosts over a range from low precipitation variation at one extreme, for example, deserts, to high precipitation variation such like in the tropics. This relationship might be related to biological cycles and a variety of features in parasitic and infectious stages that have evolved so that they are specifically well adapted to the variability of precipitation. So, prolonged drought should not be fatal for some well-adapted microbes if wet conditions are encountered once to complete their life cycle. Curiously, average precipitation was not retained as a good candidate for explaining the latitudinal gradient of pathogen species diversity except for bacteria (see Guernier *et al.* 2004). If we consider the Earth as a simple body with an environmental gradient, such as the annual precipitation range, which runs from wet and hot equatorial regions northward and southward to Arctic and Antarctic areas with harsh conditions, then distance and isolation from pathogen species-rich regions in the tropics may screen pathogen species by their extinction and colonization tendencies. Moreover, habitat suitability, for example presence of new hosts and reservoirs, and passive sampling may screen them by their habitat preference and availability, and abundance, respectively. Guernier *et al.* (2004) reached the same conclusions as Calvete *et al.* (2003) indicating that parasite species richness, their spatial distribution and organization on very different scales, climate-based forces, and the interplay between habitat conditions and host–parasite interactions might be intimately connected to generate the observed patterns of parasite species diversity.

The overall conclusion that can be drawn from this section on the latitudinal gradient in species richness for parasite and pathogen organisms is that a better understanding of parasitic and infectious diseases species diversity and community dynamics over wide ranges of spatial scales is now clearly needed. The similarity in the patterns of some parasitic or pathogen taxonomic groups and free-living organisms suggests that common mechanisms are at work. Regardless of whether the richness of parasitic and infectious diseases simply tracks host diversity or, rather, is determined to a greater extent by exogenous factors, for example, climate-forced variables, is now a challenge that needs to be pursued in parasitology and epidemiology. In addition, the significant findings illustrated in this and other sections confirm that investigations on parasite and microorganism community assemblages should also be performed at greater scales than the scale at which local variation in species richness and composition is too often examined. Integration of systematics, biogeography, population and species dynamics, community ecology, and evolutionary biology is now essential for a complete understanding of the many scaling processes affecting parasitic and infectious diseases.

2.4 Linking parasite and microorganism communities and ecosystems. Directions for further work

The results summarized above underscore the important role of large-scale determinants on local parasite and pathogen community organization and assembly processes. They suggest that the success of invasive parasite species may vary depending on how physical conditions, for example, size of the area, geographical distance from a continental source, affect the rates of colonization. Additionally, the regional effects on local parasite or microorganism species richness also tend to suggest that research should be directed at regional processes and their effect on local diversity, regional processes being just as important as local ones in setting levels of richness in parasite or microbe communities. Then, the existence of a latitudinal gradient of parasite and microbe species richness both at subregional (gut helminths in Spanish red partridges) and global (infectious diseases in human populations) scales confirms that investigations on parasites and microorganisms should expand the scale at which local variation is traditionally examined. More interestingly, the demonstration of the existence of a nested species subset pattern for human infectious diseases (also true for gut helminths in Spanish red partridges) suggests that the interplay between well-differentiated species of pathogen species within assemblages and distinctive requirements for resources, including micro- and macro-habitats, contribute to the overall nestedness pattern and species diversity we observed.

It is important to recognize that similar patterns, that is, species area, species isolation, local to global relationships, and latitudinal gradient in species diversity, have been observed for many free-living taxonomic groups (see Gaston and Blackburn 2000; Hawkins *et al.* 2003), suggesting that common mechanisms might be at work in generating the observed patterns of species diversity for parasitic and infectious agents (see previous sections). But what kinds of common properties and characteristics between, say, a virus species and a bird species, may produce similar patterns?

So far, the concern of parasitology and epidemiology has been widely aimed at defining the characteristics in which pathogens may differ from other groups, focusing on details instead of searching for similarities. One pattern that appears to be pervasive across many communities, parasites, microbes, and free organisms alike, and at different spatial hierarchical scales, is the nested species subset pattern. Nested patterns were observed in some parasitological–epidemiological studies (Guégan and Hugueny 1994; Hugueny and Guégan 1997; Guégan and Kennedy 1996; Guernier *et al.* 2004; Poulin and Valtonen 2001, 2002; Vidal-Martinez and Poulin 2003), but in many other cases communities were observed to form random, unstructured assemblages (Rohde *et al.* 1994, 1995, 1998; Poulin 1996*a,b*; Worthen and Rohde 1996). The previous sections make clear something that should be obvious, that is, that the four patterns documented above are not independent of each other. Morand *et al.* (2002) have provided a cogent explanation for the generation of nested patterns in parasite communities, thus reinforcing the importance of both spatial and demographic stochasticity in parasite species distribution and composition. Fig. 2.6 illustrates the way Morand and collaborators synthesize the hypothetical distributions of parasite species among local communities and the many factors that may be implied in shaping these communities. Considering that nested versus non-nested species patterns are strongly linked to unimodal versus bimodal species frequency distributions, respectively (Morand *et al.* 2002), the authors concluded that observed patterns should be the result of differential colonization/extinction processes acting at the level of each parasite (or pathogen) species. Differential colonization/extinction processes, also called epidemiological processes in the field of epidemiology (see Anderson and May 1991), are attributes of parasite or microbe species, and are related to birth and death processes in population dynamics (see Morand *et al.* 2002). Assemblages of microbes and parasites displaying nestedness on different hierarchical scales, ranging from within individuals of the same host population to the global scale, as shown in the present chapter, provide a strong indication that the same forces are at work across different spatial and temporal scales.

So what emerges from this concept is that both the recruitment of parasite (or pathogen) species from local (host) patches and the differential capacities of parasite (or pathogen) larval or adult forms to colonize those patches may have strong impacts on the composition and richness of those communities from the local to the global scale, and vice versa. This is an approach which is roughly similar to that adopted by metapopulation biologists (see Hanski 1999; Hanski and Gaggiotti 2004) and ecologists working on the diffusion of infectious diseases (see Grenfell and Dobson 1995; Diekmann and Heesterbeek 2000), and in which invasibility is a key factor for explaining local presence and distribution of a given species.

Invasibility is dependent on the availability of local resources and potential competition with local species, for example, presence of empty niches. In mainstream ecology (see Elton 1958), it has been hypothesized among other predictions that greater diversity should increase resistance to invasions because the levels of limiting resources are generally lower in more diverse habitats (Tilman *et al.* 1996; Knops *et al.* 1999), thus giving rise to the so-called diversity–invasibility hypothesis. A decrease in host species diversity allows remaining

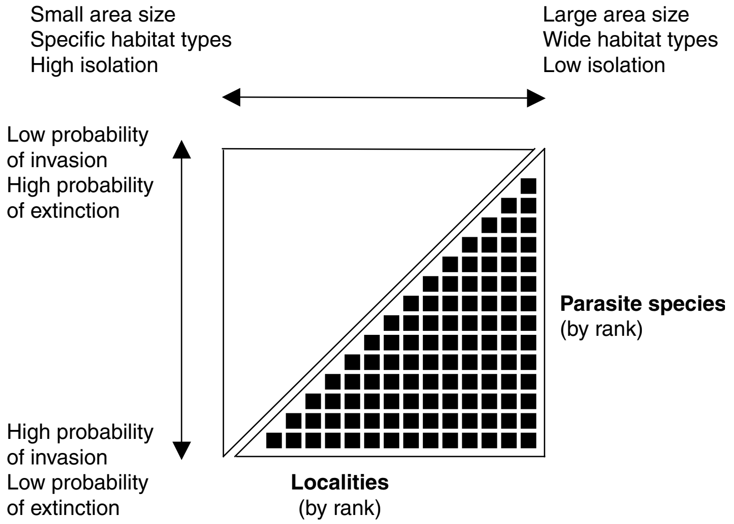

Figure 2.6 Nested (versus non-nested) species subset patterns are strongly associated with an interplay of specific characteristics of parasite (or microbe) species themselves) and local habitat conditions to sustain or not a given parasite (or microbe) species population and its life-cycle associates, for example, vectors, reservoirs. Parasite (or microbe) community ecology would benefit greatly by considering the importance of epidemiological patterns in generating the processes observed.

species to increase in abundance as a result of decreased competition for limiting ressources, a phenomenon called density compensation by ecologists (see Begon *et al.* 1996). As a result, the increase in remaining host abundances should facilitate the invasibility of parasite or microbe species (Anderson and May 1978; Burdon and Chilvers 1982; Antonovics *et al.* 1995). Indeed, host living in high densities may harbour a high diversity of parasite species (Morand *et al.* 2000; Poulin and Morand 2000; Stanko *et al.* 2002), which in turn often achieve high abundances (Arneberg *et al.* 1998*a*). Not all available results agree with this, however (Stanko *et al.* 2002). Hence, both host diversity and disease invasibility are related to host species abundances within communities (Burdon and Chilvers 1982; Mitchell *et al.* 2002). As already stated, this hypothesis has received some support in general ecology (Tilman 1997), but further work needs to be done in both parasitology and epidemiology to determine whether higher parasite (or microbe) species diversity at different hierarchical scales, that is, within-host, within-population, and within-metapopulation community dynamics protects parasite or pathogen communities from invaders (but see Torchin *et al.* 2003).

Another prediction available from the general literature is that greater species diversity of microbes or parasites should decrease the severity of each of the component diseases, a theorem which is called the species composition–disease hypothesis (see Elton 1958). This hypothesis predicts that any changes in parasite or microbe community composition within a host community should impact on the severity and virulence of one, or a group of, diseases, which then proliferate to the detriment of other parasite or microbe species. Both these hypotheses, that is, the diversity–disease hypothesis and the species composition–disease hypothesis, have received some empirical support from the plant disease literature (Knops *et al.* 1999; Mitchell and Power 2003), but they have never been tested to our knowledge in the case of both animal or human pathogens. Research on community ecology of parasite or microbe species, at the different hierarchical scales discussed in the present paper, should clearly benefit from developing both experimental designs and comparative studies to explore in greater detail the potential linkages between species diversity and composition, invasibility, and other life-history traits such as virulence.

In addition, theoretical studies on parasite (or microbe) invasibility rest upon epidemiological principles, in which the local abundance of hosts is the key determinant of whether a parasite can establish into a naïve host population (Anderson and May 1978; Burdon and Chilvers 1982; May and Anderson 1978). Within the study of human infectious diseases, recent investigations have clearly illustrated the importance of local community size for the maintenance and diffusion of, in particular, childhood diseases (see Grenfell and Harwood 1997; Rohani *et al.* 1999; Dieckmann and Heesterbeek 2000; Grenfell *et al.* 2001). Unfortunately, very few studies have gone a step further in demonstrating that higher local abundance in hosts should yield higher parasite or microbe species diversity (but see Poulin and Morand 2000).

For macroparasites, and especially for contact-transmitted microparasites, both high parasite abundance and high parasite species richness should be attained more easily at high host abundance or density. This is expected from epidemiological theory (see Grenfell and Dobson 1995) and supported by empirical studies on the determinants of parasite species richness (see Poulin and Morand 2000, and the present chapter). Indeed, host abundance/density is positively correlated with parasite (or microbe) species richness in several groups of vertebrates (Poulin and Morand 2000). This trend has yet to be demonstrated for human populations (and plant pathogens as well) in which large communities as resources should harbour and sustain a greater diversity of pathogens over space and time. Some, though very few, studies have even shown that parasite species richness covaries positively with host species richness across localities, an interesting finding that is yet to be more seriously quantified across different host taxonomic groups (Krasnov *et al.* 2004).

Any loss of host biological diversity should intuitively have a direct influence on the diversity and abundances of parasites or pathogens, and in turn on their virulence and pathogenicity within host populations. In addition, changes in host community composition should also influence the component community of parasites or microbes living there. Host species diversity should not randomly affect parasite species richness and composition as some of them will be more affected than others depending on the exact causes of diversity loss. This loss may depend on habitat fragmentation, which should impact on rare host species living at low abundance, or may be due to landscape changes, which may influence the more adapted host species, and thus will favour either the spread of rare species or invasion by exotic species (Daszak *et al.* 2001). Unfortunately, we cannot easily refer to parasitological or epidemiological studies on animals or humans that have specifically tested these different hypotheses. Further empirical studies are thus needed, which should contribute to a better understanding of how native host species and their associated parasite or pathogen species may prevent or limit the attacks of invaders (see Torchin *et al.* 2003).

In summary, there are, of course, other interesting parasitological or epidemiological patterns that are not discussed in the present chapter. However, our aim here was to argue that both parasitology and epidemiology would first largely gain from developing both a much broader perspective and a more quantitative approach, as advocated recently by both macroecologists and community ecologists. Parasitology and epidemiology are two scientific fields that have evolved with an individual-centred research perspective, and which have then concentrated their research efforts on only local phenomena over the past decades. One important message from the present work is clearly that we need to adopt a much broader research perspective in parasite (or microbe) community ecology. Second, we are also intimately convinced that a better consideration of the linkages between host species diversity and composition, and parasite or microbe species diversity and composition within communities on the one hand, and the risk of altering any (host) species and composition on host invasiveness, host defences and increase of virulence by parasites or pathogens on the other hand. We are definitely advocating here a community ecology perspective for host–parasite systems.

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