Patterns of endemism in host-parasite associations :
lessons from epidemiological models and comparative tests

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Abstract

Although the term endemism refers to restricted areas of taxa, this term is used in a different way in epidemiology and host-parasite relationship. An endemic disease refers to the maintenance of a disease over a long-term period in a limited geographic area (endemic area). In biogeographical studies, endemism refers to the organisms that are restricted to a given area. However, little is known about parasitism in endemic hosts. Here, we show how epidemiological models and the derivation of the basic transmission rate (R_0) can help to understand the pattern of parasite species richness among endemic hosts. The main prediction arising from epidemiological models concerns the host density threshold, i.e. the minimum host density that allows a disease to spread into a population of susceptible hosts. When host density, or host range, increases we can predict a concomitant increase of parasite species richness, in the case of parasites transmitted directly or though predator-prey relationship. This prediction can be tested using comparative data. These predictions are successfully tested using several data sets on parasites of marine and freshwater fish. We will show that restricted areas and/or low density is correlated with a decrease in parasite species richness. The epidemiological theory is also helpful for predictions concerning parasite and disease introductions in endemic host faunas (or isolated hosts). We emphasize why and how this endemic fauna may be susceptible to introduce pathogens and parasites.

Keywords : Host density, basic transmission rate, area range, island, parasite species richness, parasite transmission.

Introduction

Parasites and pathogens are known to potentially regulate animal populations (DOBSON & HUDSON, 1986), and numerous studies have shown how parasites can affect individual hosts and the dynamics of host population (see examples in COMBES, 1995; ESCH & FERNANDEZ, 1993; POULIN, 1998). Numerous studies have emphasized the negative influence of parasitism and/or disease in conservation biology (DOBSON & MAY, 1986; SCOTT, 1988). However, little is known on parasitism in endemic hosts.

The term endemism is used in a different way in host-parasite relationship, compared to its use in biogeography. In biogeography, endemic taxa are those restricted to a specific geographical area. The endemic status can have varying biological significance, depending on the size and location of the geographical area under consideration (CEBALLOS & BROWN, 1995). Hence, endemism refers to an epidemiological status, i.e. the maintenance over long-term of a disease in a particular locality or region. Epidemiologists speak sometimes about a hyperendemic area when the prevalence of a disease remains consistently high over time, and pan-endemy when the parasite disease has dispersed world-wide from its centre of endemism. Here, again, endemism is a relative concept.

In general, endemism is influenced by taxonomic interpretation, sampling error and human perceptions of rarity (HEYWOOD, 1995). Clearly, endemics are categorised according to their spatial distribution in biogeography whereas, in contrasts, endemic diseases rely on relative persistence over time of the species considered.

The link between epidemiology and mathematical models is important in the present paper. Indeed, various aspects of epidemiology have been investigated using mathematical modeling (DOBSON, 1988, 1989; GRENFELL, 1992; MORAND et al., 1995), for which a measure of parasite invasibility, the basic transmission rate R_0, has been derived. The basic transmission rate is defined as the average number of new infection cases that arise from one infectious host, if introduced into a population of susceptibles (ANDERSON and MAY, 1985). If R_0 is larger than one, then the parasite will spread in the uninfected population (epidemic situation) and if R_0 remains larger than one over time then the parasite is endemic of the host population. Moreover, the basic transmission rate can be used in several areas of epidemiological ecology or evolutionary biology (FRANK, 1996; van BAALEN & SABELIS, 1995).

In this paper, we try to examine several aspects concerning the ecology of parasitism in endemic hosts. For this we investigate the following questions:

What are the patterns of parasite species richness in endemic hosts?

What are the consequences of disease introduction in endemic hosts?

To answer these questions, we use predictions obtained from epidemiological modelling and these predictions are tested using recent

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comparative methods with a special emphasis on parasites of marine and freshwater fish.

We also emphasise on the ecological impact of introduced diseases in endemic hosts.

The lesson of epidemiological models : what is an endemic disease ?

As introduced above, mathematical epidemiology is of great interest to predict the ecological importance of parasitism in endemic hosts. ANDERSON & MAY (1978 and subsequent papers) investigated the epidemiology of parasites using mathematical modelling. Here, we summarise two models of direct versus indirect parasite transmission. Both models allow to calculate the basic transmission rate.

Direct transmission

A direct transmitted disease can be modeled by differential equations, which describe the susceptible population dynamics (H) and the infective population dynamics (I):

$$\frac{dH}{dt} = (a - b)H - \beta HI + rI \tag{Eq. 1}$$

$$\frac{dI}{dt} = \beta HI - (b - \alpha)I - rI \tag{Eq. 2}$$

where a and b are the growth and mortality rate of the hosts respectively, β the force of infection, r the recovery rate and α the virulence (i.e., parasite-induced host mortality).

The expression of the basic transmission rate R_0 is obtained by considering the growth rate of the disease (or the parasite population) when one infected host (or one parasite) is introduced into a population of susceptibles (see ANDERSON & MAY, 1995 for derivation).

$$R_0 = \frac{\beta H}{(b + r + \alpha)} \tag{Eq. 3}$$

We can observe from above that the condition for the spread of a parasite into a population of susceptibles ($R_0 > 1$) increases when H increases but decreases with virulence a increasing.

Vector-borne transmission

A vector borne transmitted disease can be modeled by differential equations, which describe the proportion of infective definitive hosts (x) and the

proportion of infective vectors (y) (ARON & MAY, 1982):

$$\frac{dx}{dt} = a\beta \frac{V}{H}(1 - x) - rx \qquad \text{(Eq. 4)}$$

$$\frac{dy}{dt} = ax(1 - y) - \mu y \qquad \text{(Eq. 5)}$$

where V and H are the densities of vectors and definitive hosts, β the force of infection, r the recovery rate, a the biting rate and μ the death rate of vectors.

The expression of the basic transmission rate R_0 is obtained by considering the growth rate of the disease when one infected vector is introduced into a population of H susceptibles.

$$R_0 = \frac{\beta a^2 V}{H(\mu + r + \gamma)} \qquad \text{(Eq. 6)}$$

We observe that the condition for the spread of the disease into a population of susceptibles increases when H decreases or/and V increases.

Epidemiological models and the calculation of the basic transmission rate allow to predict that there is a host threshold density, for which a parasite cannot be sustained within the host population (GRENFELL & HARWOOD, 1997). In addition, we can stipulate the existence of a positive relationship between host density and parasite species richness with the basic assumption that the epidemiological process may operate only for parasite species which are not transmitted through biting vectors.

Endemic hosts and potential determinants of parasite species richness

In practise, endemic species can be defined in relation to a particular geographic area where a population has settled on. The level of endemicity of a given taxon can be categorised according to its spatial distribution, inferred evolutionary age, and affinities with its sister taxon and abundance.

CRACRAFT (1985) stated that areas of endemism are "defined by distributional congruence of the constituant taxa" and "that two or more smaller areas of endemism may be nested within the larger one. Areas of endemism, therefore, appear to be organized hierarchically". Endemics are not randomly distributed across the earth but they tend to be more or less clustered, and they determine the existence of some centres of endemism. Patterns of congruence of endemism for different taxa thus play a crucial role in identifying those centres of endemism for instance for conservation purposes (COWLING & SAMWAYS, 1995).

According to Anderson (1994), a number of factors have been suggested to contribute to larger degree of endemism in a given area. Among them, it has

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been recognised that geographically isolated areas and biotopes such as larger islands support a higher number of endemics than islands near a continental mass or in large archipelagos and that smaller islands can support only smaller populations.

All these facts allow to propose the two following predictions:

- isolation of lands or habitats, when maintained over evolutionary time scales, may have contributed by the increase of host diversity to a concomitant increase of parasite endemics through coevolutionary processes;

- a given endemic species with a small area should include a poorer parasite species richness community in direct transmitted forms than its sister species with a wider range.
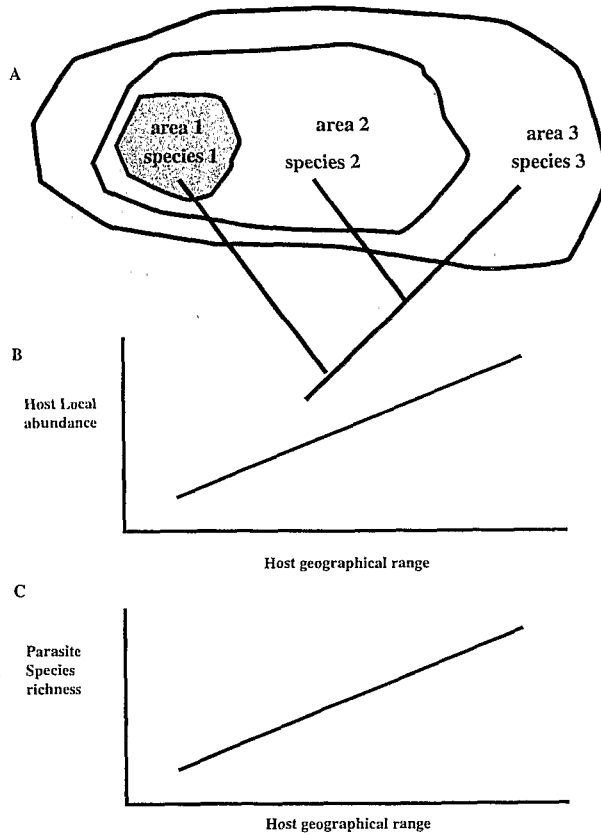

Fig. 1. Hierarchical organization of host endemism area (A), relationship between host geographical range and local abundance (B) and predictions on parasite species richness (C).

Case studies : parasites in endemic area/endemic hosts

Larger area of endemism and parasitism

Larger endemic host communities include a wider range of habitats which provide speciation opportunities for generalist parasites, e.g. species flocks of ectoparasites in species flocks of East African Cichlid fishes (comparable to neoendemics) and host refuges for parasites, e.g. parasites of marsupials in Australia (comparable to paleoendemics).

Hence, the parasite fauna of European fish is different from the parasite fauna of North American fish (MARGOLIS & ARTHUR 1980; SASAL *et al.,* 1997), and this is in part due to the fact that the two fish-compositions are distinct with a higher number of endemic forms observed in Northern America (OBERDORFF *et al.*, 1997).

The relationship between area and abundance of hosts

This pattern has been intensively studied for various vertebrate groups (BROWN, 1995; ROSENZWEIG, 1995), and a positive relationship has been demonstrated between local abundance and geographical range. Species with reduced geographic range generally tend to harbour small local population sizes. This pattern was less exemplified in the case of fish.

Endemic hosts and parasite specialisation

Host range or host specificity (LYMBERY 1989) is defined as the number of species of hosts infected by a given species of parasites. Host range may be estimated from records of host occurrence. The factors responsible for interspecific variability in host-specificity have been previously investigated in 340 species of metazoan parasite species found in Canadian marine fishes (MARGOLIS & ARTHUR 1980), and 155 species of metazoan parasites found in Mediterranean marine fishes (SASAL *et al.,* 1997). Host range differs significantly between parasitic groups. Moreover, SASAL *et al.* (1998) showed that there was no influence of host geographic localisation on the pattern of parasite specialisation (i.e. specificity) (Fig. 2).

Host spatial range and parasitism

In many host groups, the breadth of biogeographical range is constantly associated with the richness in parasite species (GREGORY, 1990; FELIU et al. 1997). The parasite species richness of North American fish shows a similar trend with a higher parasite species number observed for larger latitudinal ranges, which represents a measure of the total geographical breadth of fish (GUÉGAN & KENNEDY, 1996; MORAND, unpublished; Fig. 3)

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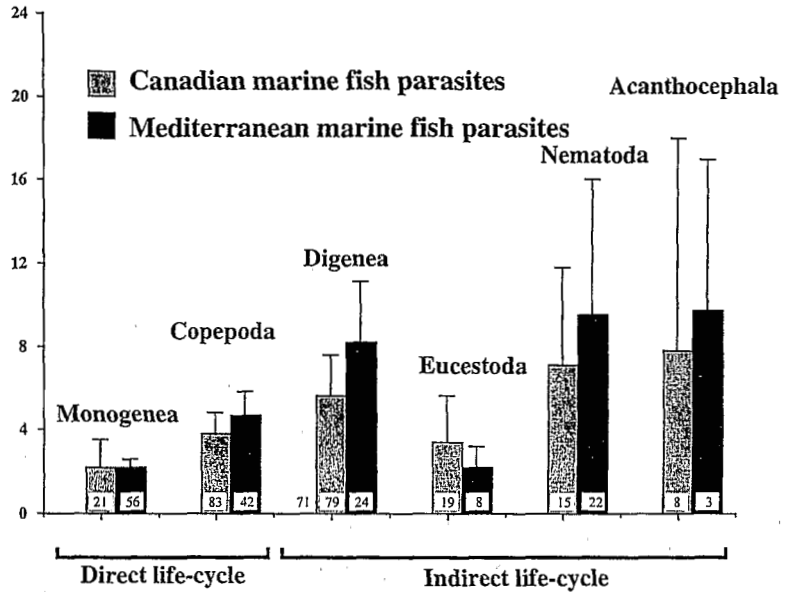per parasite species**

Fig. 2. Host range (mean number of hosts ± sd) of fish parasites of Canada and Mediterranean Sea (adapted from SASAL *et al.*, 1998).
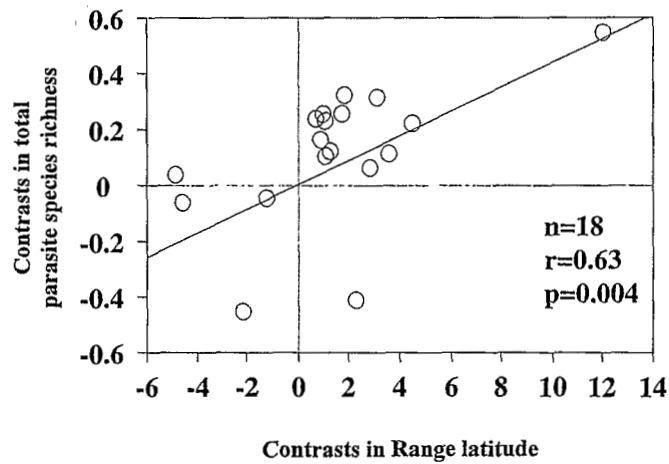

Fig. 3. Relationship between breadth of geographical range (range latitude) of North American freswater fish and parasite species richness, using independent contrasts (MORAND, unpublished).

Host density and parasitism

Several studies have shown a positive relationship between local density and geographic range size (BROWN, 1995; GASTON et al., 1998). Hence, the pattern of species richness should depend on two related factors, host density and area range. The influence of host density on parasite species richness has been highlighted by MORAND & POULIN (1998) for instance in the case of mammal parasites.

MORAND et al. (submitted) investigated the endoparasites of 21 species of butterfly fishes (Chaetodontidae) of New Caledonia. After controlling phylogenetic effects, they found that parasite species richness was correlated with host density (Fig. 4).

Finally, both host density and breadth of geographic area concur to alter the parasite species richness in endemic hosts, which are restricted to small areas.

Fig. 4. Relationship between contrasts in parasite species richess and fish density (after MORAND *et al.*, unpublished), using independent contrasts.

Further predictions

As previously emphasised, our knowledge on parasites among endemic hosts remains very scarce. However, the results of comparative analyses may be helpful to draw some general conclusions. Because parasites and pathogens are considered as a major source of host population regulation, their potential impact in biological conservation (for rare and endemic species) should be taken into consideration. Thus, an important advance in further research programs on endemic patterns and processes should be focused on the recognition that diseases may have probably contributed to rare and endemic

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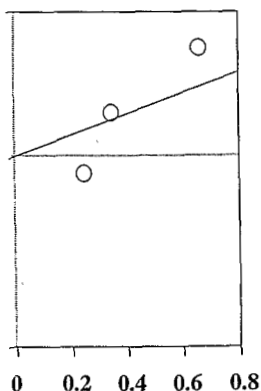
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Endemism rarity and parasitism

The main result is that breadth of geographical range seems to be a main determinant of parasite species richness. An increase of geographic range is associated with an increase of the probability to accumulate parasite species.

In many groups there is a positive relationship between the size of geographic range and the density of local populations. Thus, we can hypothesise that host species restricted to a small geographic range should harbour less parasite species because of the combined effects of reduced geographic range and small densities.

Because of the low host density, the maintenance of parasitism depends drastically on the value of R_0. We can observe for direct transmitted parasites (Eq. 3) that a reduction of parasite virulence (α) leads to an increase of R_0. We may then hypothesise that less virulent parasites should be more common in rare endemic host species.

Endemism and investment in immunity

The evolution of effective immune systems may be potentially driven by parasite pressures. The variability observed among host species in terms of immune responses should depend on different selective pressures imposed by parasites. JOHN (1995) demonstrated a correspondance between the evolution of the size of the spleen organ in birds and the prevalence of parasites. One can hypothesize that host species supporting less parasite pressures (in terms of small parasite species richness) should show less investment in immune systems compared to hosts with higher parasite pressures. An alternative hypothesis is that species living in small density (such as small areas) because of a genetic drift, should loss their potential resistance to parasitism (MØLLER & HOCHBERG, pers. com.). Accordingly, endemic species living on remote islands should harbor less parasite species richness and they should show a lower investment in immune systems/organs. There is no data, to our knowledge, to test for this hypothesis.

Endemism and parasite invasion

The potentiality for a parasite to invade a host population may be appreciated by R_0, the basic reproduction rate. This question has been previously addressed by DOBSON & MAY (1986) in relation with the complexity of the parasite life-cycle. They showed that parasites with a direct-life cycle are better invaders than parasites with an indirect life-cycle and transmitted through prey-predator relationships.

The spread of introduced direct transmitted parasites depends on host density. The spread and maintenance of a new parasite is rather difficult in an area where endemic hosts live in very low density. This leads to a new hypothesis : endemic species living on remote islands should be less invaded by direct transmitted parasites than endemic species living on large areas and in high density.

The role of parasites transmitted by vectors

The case of biting transmitted parasites has never been theoretically investigated to our knowledge. Looking at the basic transmission rate of such disease, the successful introduction is inversely proportional to host density. Hence, we can predict the inverse hypothesis as previously given for direct transmitted parasites : the spread and maintenance of a biting transmitted parasite is much easier in an area where endemic hosts live in low densities, such as endemic species living in remote and small islands.

WERNER (1968) argued that introduced diseases, such as malaria, have driven numerous endemic Hawaiian avifauna to extinction. This extinction was probably due to the introduction of the mosquito in 1826, whereas avian malaria had been introduced by migrating shorebirds and ducks coming from Alaska, Siberia, Canada and the United States. A variety of blood parasites have been recorded from these migrating birds.

The relationship between complex life-cycles and disease severity has been pointed out by EWALD (1983). He showed that microparasites with complex life-cycles are more pathogenous for man (70% of microparasite species may cause a mortality) than the species with direct life-cycles (1% only). Hence, small host populations with low genetic variability are more easily prone to extinction due to the introduction of a virulent disease transmitted through vector-borne parasites.

Confrontation of new host-parasite system and the evolution of resistance/ virulence

The presence of introduced species should not automatically be associated with pathogenicity. As reviewed by KENNEDY (1994), for 14 introduced fish parasites in Britain, only seven have been shown to be associated with some pathological effects. Hence, it is difficult to predict the outcome of the disease severity associated with introduction.

Conclusions

Our knowledge concerning parasites of endemic hosts remains very scarce. However, several studies permit to conclude that areas of high host endemism are also areas of parasite endemism, i.e. on a regional scale for freshwater fish and parasites from North America. The pattern of parasite specificity (i.e. the

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number of known host species) seems to be independent of host endemism, but rather a phylogenetic attribute of the species.

Range area is important as an explaining factor for parasite species richness, which allows to predict that endemic hosts living in restricted areas should have low densities and should harbor low diversity of parasites in terms of species richness. The results of several comparative analyses on various data sets corroborate this prediction.

Results of epidemiological models suggest that endemic hosts characterized by low densities (restricted area range) should be more sensitive to diseases transmitted by biting vectors than other diseases transmitted directly or through predator-prey relationships.

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