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# Extinction thresholds in host–parasite dynamics

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In this paper, we review the main thresholds that can influence the population dynamics of host–parasite relationships. We start by considering the thresholds that have influenced the conceptualisation of theoretical epidemiology. The most common threshold involving parasites is the host population invasion threshold, but persistence and infection thresholds are also important. We recap how the existence of the invasion threshold is linked to the nature of the transmission term in theoretical studies. We examine some of the main thresholds that can affect host population dynamics including the Allee effect and then relate these to parasite thresholds, as a way to assess the dynamic consequences of the interplay between host and parasite thresholds on the final outcome of the system. We propose that overlooking the existence of parasite and host thresholds can have important detrimental consequences in major domains of applied ecology, including in epidemiology, conservation biology and biological control.

## Introduction

The interplay between parasite species and their hosts constitutes a biological process that is both ubiquitous and of major ecological importance (Anderson 1982b, Shigesada 1997). On the level of population dynamics, these interactions are of great significance, as they influence the numbers of both species involved. Pioneering work in epidemiological modelling emphasized the consequence of the size of host populations as a main factor in disease propagation (Kermack & McKendrick 1927, Bailey 1975, Anderson & May 1978, 1979, 1981, May & Anderson 1978, 1979). One particularly important feature is a critical size or density of the host population, below which the disease cannot persist, a concept introduced by the theoretical works of Kermack and McKendrick (1927). Below this threshold, the infection would not spread and would disappear, and the few infected hosts would die, leaving a remaining healthy and uninfected host population. The existence of such a threshold has since been both widely used for theoretical studies and confirmed by empirical data and is now almost considered an intrinsic property of host–microparasite systems. In addition, this threshold has since been shown to be of major importance in the ecology and in the epidemiology of animal and human health.

Concurrently, the host population can be affected by its own size. In particular, small sized host populations may be prone to extinction due to intrinsic dynamic properties that are independent of parasitism. Indeed, several types of dynamic processes, including the Allee effect, increase the extinction probability of small populations. In many cases, these processes engender

a critical size or density threshold below which populations are almost invariably doomed. Critical thresholds for the persistence of populations have been studied mostly through mathematical models, given the extreme difficulty in accurately studying extinction processes through empirical approaches. Thresholds for both parasites and hosts have been considered extensively, but almost exclusively as separate subjects. Herein, we discuss the interplay between these thresholds, and investigate the dynamic processes that drive host and parasite populations.

Much energy has been expended in debates concerning standard definition of terms (*see* for example, McCallum *et al*. 2001). Therefore, after briefly reviewing the current state of knowledge on parasite thresholds for invasion and persistence, we present the two classical transmission terms that have been the cause of much confusion and the basis of debate (*see* for example, McCallum *et al*. 2001, De Jong *et al*. 2002, McCallum *et al*. 2002). This is important as one of these transmission terms yields a threshold below which the parasite cannot invade the population, while the other does not. Hence the need to clarify the appropriate conditions for the use of different transmission terms in models of host–parasite dynamics. We also consider the extinction thresholds that concern the host population, and the interplay of these two related types of thresholds. Finally, we discuss the possible applications of the intermingling of parasitism and host population size thresholds in ecology.

## Thresholds in parasite dynamics

The thresholds we discuss in this paper can be defined as a point of a dynamical system where any quantitative change leads to a qualitative alteration of the system behaviour. Classically, thresholds are encountered in parasite dynamics and can play a role at various stages. For instance, studies have suggested and shown thresholds for the invasion (i.e. spread) and the persistence of parasites in a population as well as for the infection of individual organisms. For the sake of clarity, the thresholds discussed in this review are briefly defined in Table 1.

### Invasion thresholds

The first type of threshold central to epidemiology concerns invasion, which is the introduction and the subsequent increase of a parasite in the host population. The concept of threshold as pertaining to the spread of infection was introduced by Kermack and McKendrick (1927), and since has been at the core of many studies concerning the regulation of either hosts or their diseases. According to this ground-breaking theory, the introduction of a few infectious individuals into a community of susceptible hosts will result in the spread of disease only if the susceptible individuals occur at or greater than a certain critical density or number. Simple epidemiological models including removal (by immunisation or mortality) and transmission terms generate a

**Table 1.** The main types of threshold employed in studies of the dynamics of host–parasite relationships, and the unit and species they refer to.

| Threshold | Unit | Species of relevance |
|---|---|---|
| Invasion | Number/density of hosts necessary for parasite spread in host population | Parasites |
| Persistence | Number/density of hosts necessary for parasite maintenance in host population | Parasites |
| Infection | Parasite infectious dose necessary for individual host infection of and/or reproduction within an individual host | Parasites |
| Extinction | Number/density of hosts necessary for host population continued existence | Hosts; for parasites, invasion or persistence are often used instead |
| Eradication | Same as extinction threshold | Same as extinction threshold. More often used when species elimination is the objective |

threshold density of susceptibility to infection. For densities below this critical value, any initial trace of infection will be removed at a faster rate than it can build up (Bailey 1964). This threshold can be defined on the basis of another important concept in epidemiology: the basic reproductive infection rate, noted $R_0$. This concept is central to the analysis of the population dynamics of host–parasite interactions and is defined as the number of individuals contracting infection from a single infectious individual, introduced in a completely susceptible host population (Knell *et al.* 1998a). A recent review on this epidemiological parameter is given by Heesterbeek (2002). For classically transmitted microparasites, this parameter can be calculated by multiplying the rate at which new infections are produced by a single infectious individual within the time period during which that individual remains infectious (Knell *et al.* 1998a). Infection can spread in the population if one contagious individual, during its infectious period, infects more than one susceptible individual, i.e. when $R_0 > 1$. As the infection rate may depend on the density of susceptible individuals in the population, the condition in which $R_0 > 1$ can be interpreted as a case when the host population exceeds a threshold density (Anderson & May 1979, May & Anderson 1979, May *et al.* 1981). For this reason, invasion may not be the best term for this threshold, nor is the sometimes used "invasibility threshold": it connotes a notion of initiation, while here invasion simply means the potential to spread further (and is still relevant even if most of the individuals are infected).

Obviously, the threshold density also depends on the characteristics of the parasite. For example, a laboratory experiment comparing the spread of two pathogens has shown that the threshold density was considerably less for one species, indicating that it would be able to persist in populations with lower densities (Knell *et al.* 1998a). In fact, the precise value of this threshold depends simultaneously on life history traits of both the host and parasite. Microparasites with low transmission efficiency, such as measles or smallpox, or with relatively high pathogenicity (i.e. inducing high mortality rates) in general will persist only in high-density populations of hosts (Anderson & May 1981). Conversely, microparasites with high transmission efficiency will be able to persist in lower density populations. However, diseases characterised by a low transmission efficiency may be able to persist even in relatively low density host populations, provided that the expected lifespan of infected hosts is long (e.g., natural and parasite-induced mortalities are both low and the average duration of the infection is long, as is the case for immunodeficiency viruses; Anderson & May 1981).

Similarly to the $R_0$ of microparasitic models, a threshold quantity has been introduced for models of macroparasitic infections (helminths), and by analogy has been named $Q_0$ or basic reproduction quotient (Roberts 1995). This value can be defined as the expected number of reproductively mature parasites produced by one adult parasite during its lifetime, in the absence of density dependent constraints (Heesterbeek & Roberts 1995). A parasite population can invade a host population only if $Q_0$ is higher than one. This threshold quantity is basic to the understanding of parasite population dynamics, including the development of methods of control in order to protect host populations (Roberts 1995).

## Persistence thresholds

Invasion addresses the events that occur in the short term immediately after the introduction of an infection. However, infection does not necessarily imply that a parasite will be able to persist over the long term (Gubbins *et al.* 2000). The persistence threshold is a host density threshold that conditions infection dynamics. This threshold is greater than the invasion threshold and hence it is more difficult to reach (Bolker & Grenfell 1996). But, whereas the invasion threshold concerns the spread of infection, the persistence threshold concerns the durability of the infection. The persistence threshold has been given a number of equivalent definitions, including the population size below which infection tends to die out in the troughs between epidemics and above which infection will persist (Bartlett 1957, Bolker & Grenfell 1996, Grenfell & Harwood 1997, Keeling & Grenfell 1997).

The persistence threshold has been central to the study of certain categories of parasites, in particular morbilliviruses, such as measles and

Phocine Distemper Virus (Grenfell *et al*. 1992, Grenfell & Harwood 1997, Keeling & Grenfell 1997, Swinton *et al*. 1998, Keeling & Grenfell 1999). In this context, this threshold has also been called the Critical Community Size (CCS), as used by Bartlett (1957) in a measles epidemics study. This threshold is related to the observation that the chance of infection "fade-out" (where fadeout is defined as a given period of time without new infections), or random extinction between epidemics, decreases as population size increases (Bartlett 1957). The recurrence of epidemics is facilitated by the continual influx of susceptible individuals, but is prevented by the random extinction of the infection. These extinctions are more likely in smaller communities (Bartlett 1957, Black 1966). For example, it has been estimated that a human community of around 250 000 individuals or more is necessary to maintain measles (Bartlett 1957).

The criteria for persistence thresholds are said to be generally more difficult to analyse than those of invasion thresholds (Gubbins *et al*. 2000). The CCS was first determined theoretically and then confirmed by analyses of epidemiological data. The value of the CCS may be governed by deterministic factors, or by one or another kind of stochastic considerations, including so-called endemic fade-out and epidemic fade-out (Anderson & May 1991). Several epidemiological parameters may be important for the determination of the CCS, including the transmission term, the host life expectancy and the parasite latent period (Dietz 1982). Whichever factor has the greatest influence will depend on the details specific to the host–microparasite relationship. For example, microparasitic infections with very short duration and low transmission efficiency will require a large population of hosts in which the rate of birth of new susceptible individuals can replace those individuals lost to infection (i.e., the threshold density for the host population will be large).

The CCS concept has been used principally in the case of measles and Phocine Distemper Virus, but it has applications in other systems. Although it is said to be of less epidemiological importance relative to microparasitic infections, macroparasite models also exhibit a critical host density below which the parasite will be unable to persist within the population (Anderson 1982b). Using the example of helminth infections, Heesterbeek and Roberts (1995) suggested that there were threshold quantities that determine whether or not an introduced infection will persist in a population of susceptible hosts. However, the distinction between invasion and persistence thresholds appears to be clearer in microparasitic than in macroparasitic models.

The thresholds for the survival of the parasite populations are separated into invasion and persistence thresholds, but both can also be called parasite extinction or eradication thresholds (Nee 1994, Bascompte & Rodriguez-Trelles 1998). Another type of threshold that concerns parasites which is linked less to their population dynamics is called the infection threshold.

## Infection thresholds

The last type of parasite threshold that can be found in epidemiological studies concerns the infection of individual hosts. For many microparasites, there is a tolerance level below which the host's immune system can resist succumbing to the infection, and above which an infection is contracted. In such models, the infection depends on the total exposure of individuals to the disease, a term including the amount of infectivity. In various experiments the probability of infection was observed to increase sigmoidally with increasing parasite dose. In a simulation model, Regoes (2002) showed that the parasite population can establish an infection only if its founder population size (the infection dose) exceeds an invasion threshold, which the author called an Allee effect. In this model, the point of inflection of a sigmoidal pattern describes well the infection threshold below which any parasite concentrations challenging the host are too low to avoid extinction. The threshold concentration that is needed by a parasite to overcome the host immunity and successfully invade the population is determined by the balance between infectiousness and virulence of the parasite. This has been described in various theoretical and empirical models (*see* references in Regoes *et al*. 2002).

Dose dependency in the rates of infection incidence has also been addressed in the context

of macroparasitic infections (e.g., May 1977, Dushoff 1996). For sexually reproducing parasites, epidemiology is characterised first by the infection, then by sexual reproduction within the host. Because many of these parasites must find mates within the host, there can be an equivalent Allee effect for the parasites in this system. There is a persistence threshold below which the macroparasite density is too low for mates to find each other within the infected host (Anderson & May 1991). The resulting mating failure can hinder macroparasite spread in the population. In addition, the parasitic load of an individual is significantly related to its infectiousness, leading to a second type of Allee effect. If parasites are too scarce or too few, the immune defences of the host have a greater chance to combat and overcome the parasites. Both processes create an unstable breakpoint phenomenon that is proportional to the degree of parasite aggregation within the host population (Anderson & May 1991), with resultant repercussions at the level of both host and parasite populations.

### Other thresholds

The theory of thresholds has been much developed since the pioneering work of Kermack and McKendrick (1927), and it would be difficult to list all existing models. However, there are several interesting extensions of this threshold theorem that deserve greater attention. For example, models involving an intermediate host or a vector, as in the case of malaria (although this was initiated in their first paper, Kermack & McKendrick 1927) and models taking into account stochasticity or the spatial dimension (Bailey 1964, 1975) are of special interest. Another interesting extension is the consideration of hosts as "habitat patches" of a pathogen metapopulation (Swinton *et al*. 1998), which leads to the generalization that the CCS is a critical metapopulation distribution of population numbers across a particular metapopulation structure (Swinton *et al*. 1998). This was elucidated in a study on Phocine Distemper Virus persistence, which is affected by a mixing effect that arises from a patchiness in some harbour seal *Phoca vitulina* populations.

We have focused here on animal species as hosts, but the criteria for parasite invasion and persistence thresholds have also been studied in the context of plant-parasite interactions (Gubbins *et al*. 2000). These thresholds are of considerable practical importance in botanical epidemiology, in particular for the prediction of yield loss, the deployment of chemical control and the implementation of biological control by introduced microorganisms (Gubbins *et al*. 2000).

Nevertheless, despite the widespread occurrence of thresholds in epidemiological models, there is an important class of exceptions: infections transmitted by intimate contact within a defined group of individuals, as is the case with sexually transmitted diseases. Under these circumstances, the threshold for infection persistence depends on the average number of sexual partners per individual, rather than the host density of classical models described above (Anderson & May 1991).

## Modelling parasite transmission

Transmission is a key process in host–parasite interactions and thus occupies a core position in host–parasites models. Whereas for macroparasites the parasite dynamics are explicitly taken into account, the modelling of microparasitic infection dynamics usually considers only the host population and the different stages according to its infection status. In the simplest classical microparasitic studies, hosts are divided into two compartments: susceptible and infected, with transmission being the main link between them. Mathematically, the transmission term is the number of susceptible individuals becoming infected per time unit.

The transmission process may be described as follows. The number of susceptible individuals contracting the infection depends on (i) the number of contagious individuals, (ii) the number of conspecifics encountered by a contagious individual, (iii) the fraction of susceptible individuals among all encountered individuals and (iv) the proportion of these encounters that result in successful transmission; (*see* Getz & Pickering 1983, De Jong *et al*. 1995, McCallum

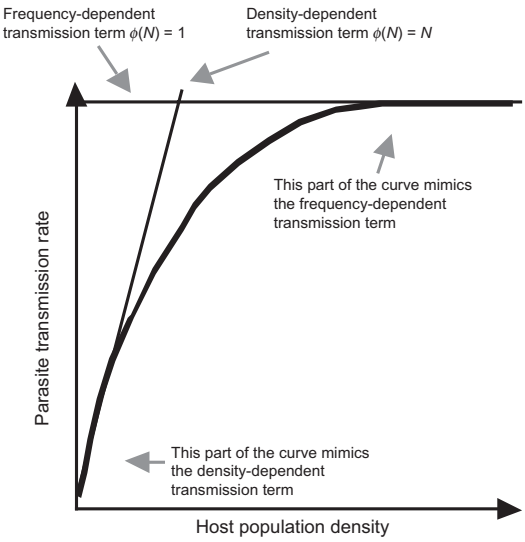


**Fig. 1.** Representation of the density-dependent and frequency-dependent terms ($\phi(N)$, *see* text, thin lines) according to population density, and of a non-linear transmission term (thick-line curve) that varies from $N$ to 1 with population density and mimics density-dependent (Mass Action) transmission at low density and frequency-dependent (Proportionate Mixing) transmission at high density.

*et al*. 2001, for quite similar partitions of the transmission term). For the sake of simplicity, infected and contagious individuals are often assumed to be the same, in both their life history traits and in their behaviour, and are noted $I$. In addition, the disease is assumed not to alter the behaviour of infected individuals. In this scenario, an infected individual encounters as many other individuals as a susceptible individual does. The relative number of susceptible individuals to all individuals encountered by an infected host equals the proportion of susceptible individuals in the population: $S/N$. The rate of transmission success following an encounter with a susceptible individual is often assumed to be a constant: $\beta$. Thus transmission is described by $(\beta SI/N)\phi(N)$, where $\phi(N)$ designates the number of contacts with other individuals per unit of time per individual. The key issue in the transmission term is how to best model point (ii) above, that is $\phi(N)$ (De Jong *et al*. 2002).

Historically the transmission was assumed to follow the Mass Action principle. This principle is a model that describes an ideal situation often assumed in chemical kinetics studies (e.g., Kermack & McKendrick 1927). According to the Mass Action principle, individuals, like molecules, would be mixed homogeneously in space and every encounter would have the same occurrence probability. Thus, the number of conspecifics encountered by an individual depends on the population density: $\phi(N)$ is proportional to $N$. This assumption leads to a transmission term called Mass Action transmission: $\beta SI$ and has been mostly used to describe air-borne diseases.

The Mass Action term is also called density-dependent (Getz & Pickering 1983, Thrall *et al*. 1993, Antonovics *et al*. 1995) since the probability of an individual becoming infected is a function of the density of infectious individuals. This name is distinguished from the frequency-dependent transmission term: $\beta SI/N$, where $\phi(N) = 1$ (*see* Fig. 1). Up to now, the frequency-dependent term, also called the Proportionate Mixing term (Dietz & Schenzle 1985, Hethcote & Vanark 1987), has been mostly used in cases of sexually transmitted and vector-borne diseases, where an individual is supposed to have a constant number of potentially infectious contacts (either direct: sexual, or indirect: via a vector). Indeed, in sexually transmitted diseases the number of infectious encounters depends on the number of sexual partners, which in turn is related more to the species mating system than to its population density (McCallum *et al*. 2001). Similarly, for vector-borne diseases, the transmission rate of the pathogen depends on the probability that the vector has previously been in contact with infected hosts, hence it depends on the proportion of infected hosts in the population (McCallum *et al*. 2001).

However, De Jong *et al*. (1995) pointed out that "density-dependence" was not the best description of the Mass Action assumption since $S$ and $I$ sometimes designate numbers instead of densities. They demonstrated that in such a case, if density is kept constant, Mass Action should be characterised by $\beta SI/N$. Consequently they called the previously named Mass Action term "pseudo mass action", while they considered the frequency-dependent as the "true mass action" term. Considering that this new terminology had brought confusion, McCallum *et al*. (2001) recommended building models based on density

rather than on numbers, thereby restricting the density-dependent term for the Mass Action assumption. Although we concur with the call for harmonisation, we remain unconvinced that population density is always more biologically relevant (or easier to measure) than population size. This concept is fundamental, as the relationship between density and population size may vary in several different ways, each of which can differentially affect how Mass Action is translated. For instance, density and population size may vary simultaneously, or one may remain constant while the other varies with the occupied area. We suggest that the first requirement in any modelling exercise should be to define precisely whether population size or density is being considered (McCallum *et al*. 2001).

It should be noted, however, that the terms frequency- and density-dependent transmission simply represent two ends of a continuum of transmission types. The pattern of transmission is likely to shift along this continuum according to the combination of densities studied and the scale of observation (Fenton *et al*. 2002). In host–parasite systems, population size is a dynamic variable, because pathogens often cause significant host mortality. In this case, systems that can be well described by a density-dependent term at low host population densities may be more correctly described by a frequency-dependent term when the host population is larger. This is due to the fact that, for very large population sizes or densities, the number of new encounters made by a single individual cannot increase linearly with population size, either because overcrowding reduces the movements of individuals, or because a related increase of occupied habitat prevents its total occupation by individuals. In fact, when density is sufficiently large, the encounter function saturates: $\phi(N)$ becomes a constant independent of population density (i.e. frequency-dependent). In these cases, a non-linear function for $\phi(N)$ that equals from 1 to N according to density would provide a suitable transmission term for all densities exhibited by a population (Hochberg 1991, Barlow 2000, Fenton *et al*. 2002; *see* also Fig. 1).

Only a few studies have assessed the applicability of simple epidemic models with available data, in particular with regards to the transmission term. In 1979, Anderson and May (1979) found a good fit between empirical data and the Mass Action transmission term of their simple model. But several more recent studies have highlighted a lack of concordance between this modelled transmission term and real data, including tests by Dwyer (1991, 1993), De Jong *et al*. (1995), Begon *et al*. (1999), Knell *et al*. (1996, 1998b) and D'Amico *et al*. (1996); but note that the frequency-dependent term also often did not provide an adequate fit of the data (*see* discussions in McCallum *et al*. 2001, Fenton *et al*. 2002). Perhaps it is best to consider a more flexible non-linear transmission term, where, depending on the host-population size, transmission changes its behaviour, from density- to frequency-dependent. Such a transmission term could be more appropriate for populations with changing sizes, either decreasing (as studied in the context of biological control or conservation biology) or increasing (as studied in the context of invading populations). Among the different transmission terms that have been previously proposed, several exhibited this pattern (*see* references in McCallum *et al*. 2001: table 1), and a test of non-linear transmission term fitness with experimental data seems convincing in this regard (*see* Fenton *et al*. 2002). However, despite the advantage of being relevant for both low and high densities, such varying terms have two drawbacks. First, they introduce non-linearities, making analytical studies markedly more difficult or even impossible. Second, they imply the choice of a function of $\phi(N)$ and therefore the models become more complex, while one may prefer to keep them simple (McCallum *et al*. 2002).

The choice of which transmission term is used to describe the dynamics of host–parasite relationships appears to be crucial, as the existence of thresholds depends on this term. Kermack and McKendrick's demonstration (1927) of a threshold was based on the study of models using a density-dependent transmission term. In contrast, Getz and Pickering (1983) showed that, depending on what exact transmission term is employed, a threshold might or might not exist. Particularly, if the transmission is expressed as a frequency-dependent term, mathematical models yield no threshold (but *see* below). Indeed, there

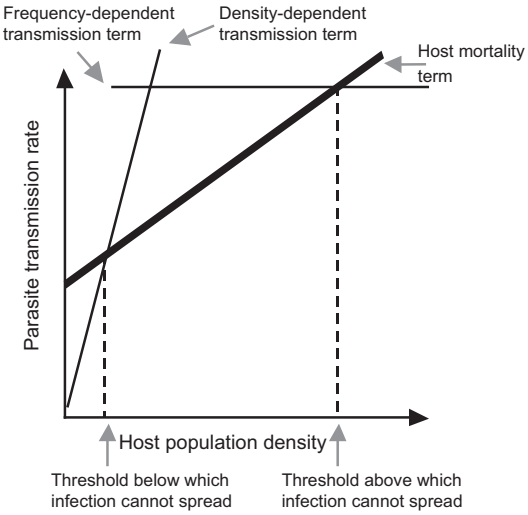


**Fig. 2.** Interactions between the mortality (thick line) and the two classical transmission (thin lines) terms of mathematical models. If the transmission term is higher than the term for mortality, then the infection spreads in a healthy population. The intersection between the two functions, when it exists, represents the threshold for infection spread. If transmission is density-dependent (respectively, frequency-dependent), values of population density above (resp., below) this threshold are those facilitating the spread of the disease.

is some interplay between transmission and mortality terms (Fig. 2). Infection spreads in a healthy population if the transmission term is greater than the term for mortality (combining natural and disease induced mortality), otherwise the infected hosts will die too rapidly to further transmit the disease. Thus infection spreads only when the transmission curve is higher than the mortality curve, and the intersection between them constitutes a threshold. In case of a density-dependent transmission, a threshold exists above which infection spreads and under which it disappears (Fig. 2). In the case of a frequency-dependent transmission term, there may be a different threshold below which infection spreads and above which it cannot spread. A non-linear transmission term would yield both thresholds, in between which infection may spread, and outside which the host population is protected from infection. In the case of the frequency-dependent model, the number of contacts between individuals is assumed to be constant: infection does not require a minimum population size to spread. On the contrary, increased density exacerbates density related mortality, and infected individuals die too rapidly to transmit infection. To our knowledge the upper threshold of frequency-dependent transmission models has not been previously discussed in the literature. This is partly because some models used a constant mortality rate, resulting in the absence of this upper threshold, or because this threshold could not exist in natural conditions. Note that for any form of density-dependent mortality (i.e. any increasing curve — not necessary represented by a straight line, as shown in Fig. 2), the results are qualitatively similar, as mortality still intersects once for each transmission term, although usually at different values.

## Thresholds in host dynamics

Although more neglected than parasite thresholds over the past half-century, thresholds that directly concern the host population, often called extinction or eradication thresholds, are also of tremendous importance. Indeed, much recent scientific energy has been expended on the study of the specific or exacerbated dynamical processes of small populations. For example, environmental variability, whether due to catastrophic events or more minor, random changes in the local environment, may hasten the extinction of a population that is not composed of enough individuals. Demographic stochasticity also weakens small populations. The small yearly variations in the numbers of deaths and births may be inconsequential when populations are large, but they may have a considerable impact on small populations. Similarly, ordinary variations in the primary sex-ratio may have dramatic consequences if the population is small (e.g., Clout & Merton 1998). Small populations are also sensitive to effects that are not directly related to dynamics, including genetic drift and inbreeding depression (Lande 1995). The most important consequence is that all these processes may contribute towards a reduction in population size, thus leading to extinction (Caughley 1994). Even though these phenomena are exacerbated in cases of small population size, they do not always translate into size or density thresholds under which popula-

tions are doomed. Nevertheless, the interplay of these processes, amongst others, has prompted population biologists to utilize the interesting and useful concept of minimum viable population (MVP). By considering extinction as an inherently probabilistic phenomenon, conservation biologists have attempted to estimate the minimal size necessary for a given population to have a particular likelihood of persisting for a certain length of time (Soulé 1996). The concept of MPV links many interacting factors, including population dynamics, environmental variations (randomness, stochasticity, catastrophes), genetics, habitat quality, metapopulation structure and fragmentation (Soulé 1996). MVP does not produce an extinction threshold and it is important not to mistake components of viability analysis, such as genetic and demographic criteria, that can yield extinction thresholds, for the MPV itself.

## Allee effect

An important phenomenon exhibiting a significant extinction threshold is the Allee effect (for recent reviews, *see* for example Courchamp *et al.* 1999a, Stephens & Sutherland 1999, Stephens *et al.* 1999; A. Deredec & F. Courchamp unpubl.). While small populations usually benefit from a high growth rate due to the lack of intraspecific competition, certain small populations are subject to Allee effects. In these cases, the populations are inhibited by low survival and/or reproduction, and thus are characterized by low to negative growth rates. On a formal level, there is a distinction between component Allee effects (that is, those positive relationships between any trait of fitness of the individuals and population density or size) and the resulting demographic Allee effect (the ensuing decrease of population growth rate at low size or density, Stephens *et al.* 1999).

The demographic Allee effect may be of varying strength, and may or may not be characterized by an extinction threshold. Although sometimes mistaken as a necessary outcome of the Allee effect, the existence of an extinction threshold is only one possible (albeit frequently encountered) consequence of the Allee effect. Wang (2001, 2002) and Brassil (2001) judiciously suggested that weak Allee effects are those that are characterized by reduced growth rates that nonetheless remain positive as density decreases. In these cases, there is no deterministic threshold. In contrast, a strong Allee effect occurs when the reduction of the growth rate drops below zero and becomes negative under a given density threshold. When a population density falls under this threshold, that population will continue to decrease and enter an extinction vortex.

There are three main biological processes that provoke an Allee effect: the reduced reproductive efficiency at low density (low probability that mates, gametes, or pollinators/flowers will encounter each other), the failure of an adequate modification of the habitat (e.g., of the soil, in the case of plants), and the decrease of beneficial social interactions (as in the case of cooperative species). The Allee effect seems to be widely spread. It occurs in numerous species, ranging from insects (Fauvergue *et al.* 1995) to large mammals (Larkin *et al.* 2002). Although empirical demonstration of this effect remains uncommon, many theoretical studies have demonstrated its heavy impact on population dynamics (Dennis 1989, Lewis & Kareiva 1993, Amarasekare 1998, Courchamp *et al.* 1999b, Gyllenberg *et al.* 1999, Wang *et al.* 1999, Courchamp *et al.* 2000a, Courchamp *et al.* 2000b, Brassil 2001, Keitt *et al.* 2001, South & Kenward 2001, Wang & Kot 2001, Dennis 2002, Etienne *et al.* 2002, Ferdy 2002, Wang *et al.* 2002).

## Spatial thresholds

While population biologists have focused on the minimum population size or density, community ecologists have mainly focused on the minimum size of areas necessary for system viability (Soulé 1996). The concept of an extinction threshold is also used in spatial ecology, where it refers to the minimum amount of habitat required for a population of a particular species to persist in a landscape (Lande 1987, Hanski *et al.* 1996, Hanski & Ovaskainen 2000, Fahrig 2002). Metapopulation theory has been used to estimate the minimum amount of suitable habitat (MASH) necessary for a population to persist (Hanski & Gilpin 1991). The related Minimum Area Requirement (MAR) is a spatial equivalent of MPV (Soulé

1996). Spatially explicit models, or those using migration rates, usually predict a higher extinction threshold, suggesting that when dispersal is spatially constrained, more habitat is required for population persistence (Bascompte & Sole 1996, Pagel & Payne 1996, Hill & Caswell 1999). Depending on whether their approach is essentially deterministic or stochastic, modelling studies depict the extinction threshold as the minimum amount of habitat below which either the equilibrium population size is null, or the probability of long-term population survival is lower than one (Fahrig 2002). Empirical studies use a somewhat different definition of threshold: an amount of habitat below which probability of occupancy declines precipitously (Fahrig 2002). The main factors thought to determine the spatial extinction threshold of a given organism are its reproductive rate, its rate of emigration from the habitat, habitat fragmentation and survival rate of the organism in non-habitat area (Fahrig 2001). The value of this threshold is increased by Allee effects caused by the difficulty of finding a mate, edge effects resulting from the finite extent of regions containing suitable habitat, and the influence of stochastic fluctuations in life history parameters, usually caused by regional environmental variations (Lande 1987).

There are of course interactions among these dynamic processes; for example, environmental stochasticity may push some populations below the Allee limit, or perhaps even rescue other populations that have fallen below it. Similarly, density and migration play different roles for the Allee limit and for spatial thresholds, often revealing complex relationships. But interactions that hold the most interest are certainly those between host and parasite thresholds, since these two types of threshold have opposite influences on the host population: one is detrimental (e.g., Allee limit) and the other is beneficial (e.g. parasite invasion or persistence thresholds), because it contributes to its resistance to disease.

## Interplay between host and parasite thresholds

In case of populations subject to an Allee effect, low density is synonymous to low infection rates (and possible parasite elimination) but also to high risks of extinction. In fact, the fate of infected populations that are subject to an Allee effect depends upon the respective position of the Allee limit and the infection threshold (Fig. 3). Stochastic considerations aside, if the Allee limit is below the infection threshold, a decrease in density could help eliminate the parasite, without endangering population survival. If the Allee limit is above the infection threshold, however, the host population is unlikely to get rid of the disease by decreasing in size (e.g. due to the action of the parasite), because the first encountered threshold on the declining curve is fatal to the host but not to the parasite. Obviously, the closer the two thresholds are to each other, the less pertinent is the question of their relative position, especially in presence of stochastic variations. Environmental stochasticity will increase not only the risk of passing under a threshold but also the chances of recovering after passing below it.

Two points concerning these thresholds merit further discussion. First, parasites may debilitate hosts in such a way that a significant part of the population is effectively removed from the viable population (i.e. for reproduction or social interactions), even if those debilitated individuals remain alive. In this case, a simple census of total individuals present in the population may falsely give the appearance that the population is further away from the Allee limit than it actually is. Second, the dynamics of both small-sized populations and infected populations may act on two different time scales, thus reducing the value of making direct comparisons. Environmental or demographic stochasticity, in addition to some Allee effects that impact survival, generally have immediate effects. In contrast, dynamic processes related to the genetic consequences of small population size and Allee effects that affect reproduction will have effects on a greater time scale (at least one generation). Meanwhile, parasites will often have immediate effects. The differences on the temporal scale between these processes will be reduced in species with short generation times (such as insects).

Thresholds play an important role in several domains of applied ecology related to population dynamics, where recognizing the interplay between thresholds of parasites and of hosts

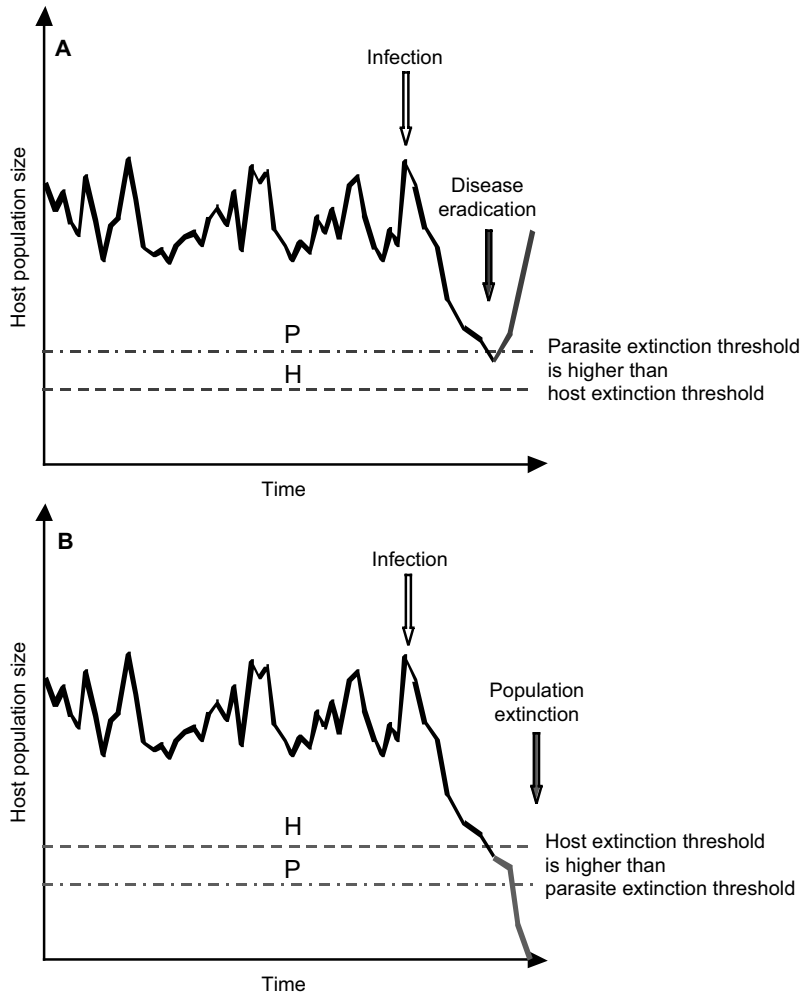


**Fig. 3.** Importance of the relative position of the host and the parasite extinction thresholds for the persistence of one or the other species. — **A**: the parasite threshold is higher than that of the host, and thus a decline will eradicate the parasite. — **B**: the host extinction threshold is the highest, and a decline will doom the host population. Situation **A** is sought in epidemiology and conservation biology, while situation **B** is sought in biological control.

may turn out to be crucial. In particular, we now briefly highlight three major fields in which parasite thresholds, host thresholds, or both are particularly significant: epidemiology, conservation biology and biological control.

## Animal and human health

The focus of studies on the dynamics of parasites may be divided into three main categories: parasites affecting human populations, those affecting wild or feral animals and those affecting farmed animals. The dynamics of the host population (i.e. constant, density dependent, etc.) is quite different for each of these three cases. Yet, the existence of infection thresholds has resulted in the development of common strategies against epidemics in all three categories. Apart from the use of quarantine, which is rarely possible in natural populations, the only way to eradicate epidemics consists in driving the infection below its invasion or its persistence thresholds. This is accomplished by decreasing the density of susceptible individuals below the parasite invasion threshold, such that the average number of effective transmissions produced by an infected individual is below one, which prevents infection from spreading. Reducing the amount of susceptible individuals can be achieved by their removal, or culling (Lafferty & Gerber 2002). For human populations or threatened species, where culling is not possible, the strategy consists in reducing the fraction of the susceptible population by immunizing them against the disease (e.g., Anderson 1994, Gren-

fell & Harwood 1997). Much theoretical work has been conducted to compare the effectiveness of these two different options, for example in rabies (Anderson 1982a, Barlow 1996) or bovine tuberculosis (White & Harris 1995, Smith & Cheeseman 2002). Theory predicts that the Critical Community Size will increase as a vaccination program is undertaken in the population (Dietz 1982, Anderson & May 1991, Grenfell & Harwood 1997) and this has been confirmed by the success of some vaccination programs. The history of public health initiatives has indeed shown that vaccination has a tremendous potential, although some diseases, such as measles, continue to resist eradication efforts (e.g., Bolker & Grenfell 1996, Keeling & Grenfell 1999).

However, these strategies of disease control may present some risks, particularly in cases where possible host thresholds have not been taken into account. For example, as quarantine forbids interactions between certain individuals and the rest of the population, it can reduce the effective size of threatened populations, thereby pushing it closer or even under its extinction threshold. Culling must also be employed with caution, for if it is employed carelessly, it could push the host population under both the parasite and the host extinction thresholds. Vaccination can be an option in farmed animals but there is no evidence that it is effective in protecting threatened mammal populations, partly because an understandable unwillingness to leave some unvaccinated animals as control prevents effectiveness monitoring (Woodroffe 1999, Lafferty & Gerber 2002). Moreover, vaccination has sometimes been rejected by conservationists, because it was too expensive, logistically difficult (especially when multiple doses are necessary) or considered unsafe for the animals (Woodroffe 1999). The latter was the case, for example, with Canine Distemper Virus vaccines in programmes to protect Ethiopian wolves following the debate over the problems encountered by African wild dogs and black-footed ferrets (Woodroffe 1999).

## Conservation biology

Conservation programs involve endangered populations that are often declining and thus possibly close to extinction thresholds. An objective of most conservation programs is to increase population size in order to keep it as far as possible above their critical size. However, as we have seen, an increasing population can push the population above the extinction threshold of one or several parasite species, and thus generate new and potentially disastrous infections.

Parasitism has a large impact in biological conservation (Minchella & Scott 1991, Viggers *et al*. 1993, Gulland 1995, McCallum & Dobson 1995, Saether *et al*. 1996, Woodroffe 1999, Sasal *et al*. 2000, Lafferty & Gerber 2002). Diseases may be a significant cause of population collapse (Crawley 1992, Lafferty & Gerber 2002) and population extinction, in particular of small ones (Woodroffe 1999). For example, parasites may keep populations at a size where they are vulnerable to the host population thresholds mentioned above. Disease may also compromise conservation projects such as reintroductions, translocations or restocking programmes (Viggers *et al*. 1993). These activities illustrate particularly well the contrasting effects of population increase on parasite and host extinction thresholds, and the resultant potential dangers to the population. The enlargement of populations may favour the spread of infection, either of already existing parasites that were kept below invasion thresholds, or of new parasites that were introduced with the reintroduction activities (Lafferty & Gerber 2002). The debilitation and stress related to captivity and subsequent release into a new environment also increase the risk of epidemics among the reintroduced or reinforced populations (Scott 1988, Lafferty & Gerber 2002).

The old controversy between creating a Single Large reserve Or Several Small ones (SLOSS) is pertinent in the case of parasites: a single large population would be more easily threatened by epidemics, while several small populations would be susceptible to the threat of extinction, because they will be closer to their extinction thresholds. The same type of predicament concerns the establishment of connections of habitats (and thus of populations) by corridors: while they can protect small populations from extinction by acting as artificial enhancers of population sizes, at the same time the corridors render them more vulnerable to existing

parasites, or to parasites initially present in only one population (Hess 1994, Hess 1996, McCallum & Dobson 2002). The quarantine strategy mentioned above is one possible solution advocated in this context (Hess 1996). Because increasing population size can save populations from extinction thresholds while also making them more susceptible to parasites that have been concurrently (and unwittingly) unleashed, conservation managers have much to gain in paying greater attention to extinction thresholds.

### Biological control

Biological control is the use of living organisms as pest control agents. One common action of biological control is to introduce a natural enemy into the population targeted for reduction or elimination (Waage & Greathead 1988). Here, parasites play a double role: they are important control agents, but they can also be hindrances to the control program if they affect the control agent, either a predator or a parasitoid. It has been argued that ecological theory has not been useful in guiding the choice of natural enemies or in developing release plans (Murdoch & Briggs 1996). In particular, until very recently there were no theoretical rules for decisions concerning the number and size of released biological control agents, in the context of avoiding extinction thresholds (Grevstad 1999).

As control agents, parasites are exploited for their potential to spread in the pest population. This propagation is possible only if the host population exceeds the infection threshold. Whereas this could be easily achieved during the first stages of the epidemics, it may become less propitious as the host population is reduced and the parasite extinction threshold is approached. As feral cat density on Marion Island decreased in response to the introduction of Feline Panleucopenia Virus, the efficiency of this control agent decreased and stabilised at a level of about 20% of the original feral cat population (van Rensburg *et al*. 1987, Bester *et al*. 2000). If the host population is sensitive to its own extinction threshold, due to an Allee effect, then the objective of the introduced parasite is more likely to succeed, as it must only reduce the host population below this threshold. Again, this is possible, in theory, only if the host extinction threshold is above the parasite extinction threshold. Criteria for the choice of a predator or parasitoid species as a pest control agent should thus include consideration of the population size of optimal efficiency and possibly extinction thresholds, as well as possible parasite thresholds that could hinder their efficacy as control agents (Hopper & Roush 1993).

## Conclusion

Nee (1994) states that the extinction threshold for a population can be understood simply as the unused amount of its limiting resource. This represents susceptible individuals in epidemiology, prey in the case of biological control by predators or parasitoids, and habitat or the number of available mates in conservation biology. The focus of attention of these major domains of applied ecology is driven by the same concern: the eradication of species (Nee 1994, Bascompte & Rodriguez-Trelles 1998). It has long been recognised that extinction or eradication thresholds are of tremendous importance whether one is interested in the control of parasites (epidemiology, conservation biology) or in the control by parasites (biological control). What has perhaps been overlooked in the past is that the opposite effects of interacting host and parasite thresholds may have important and fascinating implications for the study of host parasite dynamics.

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