Wildlife Disease Ecology

Linking Theory to Data and Application

Just like humans, animals and plants suffer from infectious diseases, which can critically threaten biodiversity. This book describes key studies that have driven our understanding of the ecology and evolution of wildlife diseases. Each chapter introduces the host and disease, and explains how that system has aided our general understanding of the evolution and spread of wildlife diseases, through the development and testing of important epidemiological and evolutionary theories.

Questions addressed include: How do hosts and parasites coevolve? What determines how fast a disease spreads through a population? How do coinfecting parasites interact? Why do hosts vary in parasite burden? Which factors determine parasite virulence and host resistance? How do parasites influence the spread of invasive species? How do we control infectious diseases in wildlife? This book will provide a valuable introduction to students new to the topic, and novel insights to researchers, professionals, and policymakers working in the field.

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Preface: Wildlife Disease Ecology

KENNETH WILSON, ANDY FENTON & DAN TOMPKINS

Introduction

Infectious diseases are ubiquitous and account for some of the most dramatic impacts in human history. These include The Black Death, caused by the bacterium *Yersinia pestis*, which killed at least 25 million people across Eurasia between 1347 and 1352 (Cohn, 2002); the Spanish Flu pandemic of 1918, caused by a highly virulent form of the influenza virus, which caused the deaths of 25–50 million people (Taubenberger, 2006); and, more recently, the global AIDS epidemic, caused by the human immunodeficiency virus (HIV), which is responsible for the mortality of an estimated 35 million people worldwide since its emergence in the early 1980s (Fajardo-Ortiz et al., 2017). In many instances, microparasites like influenza mutate and evolve over time into new lethal forms, re-emerging as new epidemics or global pandemics (Nichols, 2006).

However, infectious diseases are not exclusive to humans; wildlife, both animals and plants, experience potentially huge burdens of disease. Indeed, many of the most devastating infectious diseases of humans, including all those mentioned above, had a wildlife (zoonotic) origin. Infectious diseases are a significant driver of global biodiversity loss, illustrated by the amphibian species extinctions and population declines globally caused by the fungal disease chytridiomycosis (Fisher et al., 2009), and more localised impacts such as the loss of much of the native Hawaiian avifauna due to avian malaria and pox (Atkinson & LaPointe, 2009). With ongoing wildlife disease emergence, arising primarily from increasing human-driven global connectivity (Tompkins et al., 2015), the understanding for management that wildlife disease ecology gives has never been more important.

Not all parasites, though, cause high levels of mortality, but instead cause significant morbidity in terms of reduced growth rate and fertility. This is particularly true of macroparasites, such as gut helminths and ectoparasites, where morbidity increases as a function of parasite load (Wilson et al., 2002). Even when not resulting in extinctions or declines, wildlife diseases can have

profound ecological and evolutionary impacts on their wildlife hosts, causing the evolution of costly resistance mechanisms, potentially driving sexual selection for exaggerated traits, altering host population dynamics, and shaping the structure of ecological communities. There has thus been a considerable effort to understand and address disease across a wide range of wildlife systems in which management is important for both conservation and public health reasons. Many of the most influential studies of infectious diseases in wildlife systems have achieved their status by coupling intensive observational and experimental studies together with a strong connection to mathematical models of infectious disease dynamics. In recent decades this has allowed the amendment, advancement and refining of earlier theories and ideas.

Mathematical models have played a key part in our understanding of human infectious diseases and their control since the first epidemiological models developed over a century ago by people such as Ronald Ross and George Macdonald (Smith et al., 2012). In the late 1970s and early-mid 1980s, Roy Anderson and Robert May applied the same basic principles to the diseases of wildlife (Heesterbeek & Roberts, 2015). Those models allowed simple exploration of key aspects of host–parasite ecology; for example, by laying bare the potential for parasites to regulate host populations, or to drive cycles in host population dynamics. Since then, a burgeoning array of mathematical models have been developed for wildlife diseases, parameterised with empirical data collected during meticulous field and laboratory studies. The aim of this book is to present a core group of those studies, some of which are now decades old, highlighting the connection of these studies to general epidemiological and evolutionary theory, and emphasising the contribution they have made, and continue to make, in advancing our understanding of the spread and impact of infectious diseases more generally.

This book is aimed at researchers working in the field but we specifically asked authors to write their chapters in an engaging style that would also appeal to non-experts such as advanced undergraduates. To help the novice reader, we have included a Glossary of Terms (page xvi) and provide both technical Abstracts and non-technical Lay Summaries (available online at www.cambridge.org/9781107136564).

Book structure

The book is loosely divided into three parts depending on the scale of the interactions that are the main focus of each chapter. Perhaps inevitably, given the inherent multi-scale nature of disease ecology (Johnson et al 2015), no chapter is limited in scope to their ‘assigned’ part, but this grouping was chosen as an attempt to bring together chapters that deal with similar concepts, and is perhaps preferable to (or at least no less arbitrary than) one based on taxonomy or geography.

Part I deals with our understanding of within-host processes, such as interactions between different parasite strains and species within individual hosts, the evolution of parasite virulence, host resistance and the immune system, and host–parasite coevolution. Part II explores our understanding of between-host processes, such as the roles that parasites play in regulating and driving host population dynamics, the factors influencing parasite transmission between individuals, and herd immunity. Part III expands out to interactions at the host community and landscape scale, including the effects of climate and seasonality, trophic interactions, host migration, and spatial and multi-host dynamics.

Case studies were selected for inclusion based on their contributions to the field of wildlife disease ecology, and to cover the comprehensive range of theoretical concepts in disease epidemiology, evolution, and ecology. To illustrate the ubiquity of wildlife diseases, we chose a broad variety of host taxa (including plants, insects, gastropods, crustacea, fish, amphibia, birds, and mammals) and geographical regions (Europe, Americas, Australasia, Asia, and Africa). We wanted authors to focus on their particularly well-understood study systems but also to place their work in the broader context of other wildlife disease ecology studies; we also asked them to reflect on why their studies had been so successful, to discuss the history and natural history of the system and, where appropriate, to highlight its applied relevance.

Although all the case studies are guided by theoretical considerations, the extent of the system-specific mathematical modelling varies. We asked authors to reflect on the reasons for this, and to identify areas for future empirical and modelling work, particularly where this might benefit from advances in methods and theory (such as novel molecular or statistical approaches, new remote sensing and biologging technology, and enhanced computational capacity).

Some concluding remarks

Several common themes emerge from this book. First, our understanding of wildlife disease ecology is greatly enhanced by studies that: (i) collect long-term observational field data, providing time series and accumulated knowledge of the system (i.e. most of the chapters in this book); (ii) combine observational data with well-designed field and laboratory experiments, especially those that include experimental perturbations such as short-term parasite removals/additions (e.g. Chapters 3, 4, 5, 8, 10, 12, 14, 21); (iii) have a strong theoretical component and integrate empirical data with statistical, simulation and/or mathematical models (again, most of the chapters in this book); (iv) take advantage of new and developing technologies, such as modern molecular approaches to characterise host/parasite genetic variation (e.g. Chapters 1, 2, 4, 10, 13, 15, 18), or sophisticated statistical approaches, particularly allowing the rigorous fitting of models to data (e.g. Chapter 8).

A second theme to emerge is that the types of questions that can be addressed, and their success, are often determined by the specific natural history of the system and the logistical constraints they present. For example, the ladybird system provides an ideal opportunity for studying sexually transmitted infections (STIs) in the field because mating contacts and the STI (an ectoparasitic mite) are both easily scored visually (Chapter 7). Likewise, the fact that the snail *Potamopyrgus antipodarum* has both sexual and asexual (parthenogenic) females, often in the same lake, makes it an ideal system for studying the interaction between mode of reproduction and parasite resistance (Chapter 2). Isolated populations, such as the Soay sheep on St Kilda (Chapter 4) and the reindeer on Svalbard (Chapter 14), provide relatively simple ecological systems in which to study wildlife diseases in the absence of significant pressure from predators or competitors (although the logistics of getting there can often add an extra layer of complexity!). Most ecological systems, however, are not this simple and some, such as the three aquatic systems in this book (Chapters 9, 16 and 19), as well as the monarch butterfly system (Chapter 17), seem to lend themselves particularly well to studying these multi-trophic interactions.

A third theme to emerge is the key role that variation and heterogeneity play in determining wildlife disease dynamics at all scales. The theory of host–parasite interactions initially developed in a 'mean field' manner, such that accompanying mathematical models frequently contained simplifying assumptions and parameter values expressed as population or subpopulation averages. This was not solely due to the developmental stage of the field of study, but also to the data requirements to accurately parameterise more complex models. Many of the long-term studies presented here show that when sufficient data are amassed, allowing more complex models to be employed, our understanding of wildlife disease dynamics is improved through the realisation of how variation alters previous mean field predictions. In turn, this allows more accurate projections, and more effective management, of wildlife disease impacts.

This consideration of management illustrates a final theme to emerge from this book – while some systems are ideally placed to ask interesting and fundamental questions about wildlife disease ecology and evolution, others have the added attribute that they also have significant applied relevance. For example, a number of the study systems in this book focus on emerging diseases that have conservation and policy relevance (e.g. Chapters 5, 9, 11, 13, 15, 17, 18, 20) or impact on the management of harvested stocks (e.g. Chapters 8 and 19).

With increased international movements and global change (climate, land use, population growth, etc.), we are likely to see continued emergence of infectious diseases in humans, livestock and wildlife, and further exchange of infectious diseases between them. Based on the work presented in this book, it seems to us that the ongoing development and application of new tools and

approaches makes the field of wildlife disease ecology better placed than ever to understand and overcome these challenges.

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Glossary of Terms

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Term	Definition
Acquired immunity	***Antigen***-specific immunity gained from prior exposure to that ***antigen***.
Adaptive immunity	The components of the vertebrate ***immune system*** involved in developing ***acquired immunity***.
Aetiology/aetiological agent	The cause/causative agent of a ***disease***.
Agent-based (or individual-based) models (ABMs or IBMs)	Computational simulation models in which individuals or groups of individuals ('agents') are explicitly modelled, for example to consider how variation in states, actions or experiences between those individuals combine to affect population-level dynamics.
Aggregated parasite distribution	The often-observed highly skewed distribution of ***macroparasite*** burdens among ***hosts***, characterised by high variance: mean ratios, such that typically most hosts are observed to have relatively light (or zero) burdens, but some hosts have very high burdens. The observed distribution is often described statistically by a ***negative binomial distribution***.
Akaike Information Criteria (AIC), Watanabe–Akaike Information Criteria (WAIC), Bayesian Information Criteria (BIC), etc.	Measures of the statistical fit of a model to data that take into account the goodness of fit (often related to the likelihood of the data given the model parameters) and model complexity (penalising in some way models with higher numbers of parameters).

Allee effect	Demographic and behavioural changes that cause fitness to increase with population density (positive density dependence) at low population density.
Antibody	Large protein, specific to a given ***antigen***, used as part of the vertebrate ***immune system*** to fight certain parasites containing that antigen.
Antigen	A foreign substance which stimulates an immune response.
Antimicrobial peptides (AMPs)	Peptides produced by all classes of ***hosts*** (vertebrates, invertebrates and plants) as part of their innate immune system, to combat bacteria, viruses and fungi.
Apex predator	The predator species at the top of a food chain.
Apparent competition	A negative interaction occurring between two or more ***host*** species, mediated by a shared natural enemy
Arrested development	A life-cycle stage of some helminth ***parasites*** in which infecting worms undergo a temporary cessation of development or dormancy inside the host.
Assortative contact	The tendency to make contact with individuals of the same type as self. Contrast with ***disassortative contact***.
Basic reproductive number/ratio/rate (R_0)	A measure of the ***parasite's*** maximum potential to spread through a ***host*** population. Defined differently for ***microparasites*** (the number of secondary infections produced by a single primary infection in an otherwise wholly ***susceptible*** host population) and ***macroparasites*** (the number of mature parasite offspring produced by a single mature parasite in a wholly ***susceptible*** host population)
Capture–Mark(–Release)–Recapture (CMR or CMRR)	The recapturing of previously marked individuals to allow estimation of (for example) population sizes, and (state-dependent) survival, state transition and recapture probabilities.

Coefficient of variation	A measure of relative variability, defined as the standard deviation of a trait divided by its mean, producing a scalable measure of variation.
Coinfection (or co-infection or polyparasitism)	Simultaneous infection of an individual ***host*** by multiple ***parasite*** genotypes (intraspecific coinfection) or species (interspecific coinfection).
Community assembly	The order in which the species in an ecological community (e.g. a parasite ***infracommunity***) assemble, and the underlying processes determining that order.
Compartmental model	Mathematical model of ***host–parasite*** population dynamics, in which the abundances of ***hosts*** and/or ***parasites*** are represented as 'compartments', with flows of individuals into and out of compartments being determined by epidemiologically important processes (births, deaths, ***transmission***, recovery). See ***SIR, SEIR, SIS, etc. models***.
Competitive release	The expansion or increase in abundance of a competitively inferior species due to suppression or removal of a dominant competitor.
Contact network	Who contacts whom at an individual level, defined in terms of nodes (the individuals on network) and edges or links (the contacts between nodes); often used within a ***network-based model***.
Covert infections	Non-lethal ***infections*** that may be hard to detect, but which can contribute to overall ***transmission*** and persistence of the ***parasite*** in the ***host*** population.
Cytokine	Small signalling molecules secreted by cells of the ***immune system***.
Density-dependent prophylaxis	A phenomenon where ***hosts*** invest more in defence at high densities.
Density-dependent transmission	***Transmission*** in which the *per-capita* rate of acquisition of new infections increases

	with ***host*** density. Contrast with ***frequency-dependent transmission***.
Deterministic	A system or modelling framework which does not incorporate any random components. Contrast with ***stochastic***.
Dilution effect	The phenomenon by which low competence ***host*** species reduce infection risk for other potential host species, through the removal of ***parasite*** infective stages.
Directly transmitted parasites	***Parasites*** which transmit from one ***host*** to another, possibly via an environmental stage, but without involvement of an alternative, intermediate, or vector host species.
Disassortative contact	The tendency to make contact with dissimilar individuals, those of the opposite type to self. Contrast with ***assortative contact***.
Disease	The pathological, detrimental impact of parasitic infection on ***host*** health.
Disease triangle	A concept that recognises that the occurrence and outcome of ***infection*** depends on the interaction between the ***parasite,*** the ***host*** and the environment they occur in.
Effective partner acquisition rate	A measure of partner acquisition for a ***sexually transmitted infection (STI)***, measured from the perspective of the infection, rather than ***hosts*** generally, which includes both mean and variation in partner acquisition.
Emerging infectious disease (EID)	An ***infectious disease*** which has recently emerged in a novel ***host*** species or population.
Endemic (infection)	An ***infectious disease*** regularly found infecting a population of ***hosts***.
Enemy release hypothesis	The hypothesis that ***invasive alien species*** perform better in their introduced habitat because they have been introduced without natural enemies (predators and ***parasites***) from their native range.

Enzootic	An ***infectious disease*** regularly found infecting a population of wild animal ***hosts***. Contrast with ***epizootic***.
Epidemic	A rapid increase in the occurrence of an ***infectious disease*** in a population.
Epizootic	An ***infectious disease*** that suddenly increases in frequency in a wild animal population. Contrast with ***enzootic***.
Extirpation	The local extinction of a species from a given location.
Faecal egg count (FEC)	The number of eggs of a gastrointestinal ***parasite*** counted from a faecal sample of the ***host***, often used as an indirect measure of the ***infection intensity*** of the host.
Force of infection	The *per-capita* rate at which ***susceptible*** individuals become infected.
Frequency-dependent transmission	***Transmission*** in which the *per-capita* rate of acquisition of new infections is independent of ***host*** density, but increases with the frequency of infection in the host population. Contrast with ***density-dependent transmission***.
Functional response	The relationship between resource availability and consumer ingestion rate.
Gene-for-gene model of host–parasite compatibility	Genetic model of ***host–parasite*** compatibility in which there is a universally infective ***parasite*** genotype that experiences high infection rates across all ***host*** genotypes. Contrast with ***inverse gene-for-gene, matching alleles*** and ***inverse matching alleles models of host–parasite compatibility***.
Handicap principle	The hypothesis that the honesty of extravagant sexual signals of quality relies on costs (possibly mediated by parasitic infection) involved in their production or maintenance. See also ***Immunocompetence Handicap Hypothesis (ICHH)***.
Healthy herds hypothesis	The hypothesis that predators selectively remove ***diseased*** individuals, thereby

	raising the overall health of the remaining prey population.
Heterogeneity (e.g. in contacts, susceptibility, etc.)	The occurrence of differences among individuals or groups of individuals that result in ***transmission*** deviating from assumptions of ***mass action***.
Horizontal transmission	***Transmission*** occurring between host individuals that does not involve direct mother-to-offspring (***vertical***) transmission.
Host	An organism infected by a ***parasite***.
Immune priming	The reduction in ***host*** susceptibility to infection due to prior exposure to the same ***parasite***.
Immune system	The collection of cells and molecules that a ***host*** uses to fight infection.
Immunocompetence Handicap Hypothesis (ICHH)	An extension of the ***handicap principle*** of the evolution of extravagant sexual signals, which argues that androgens (e.g. testosterone) mediate a trade-off between enhanced sexual behaviours or signals and ability to resist ***parasites*** via ***immunosuppression***.
Immunomodulation/ immunosuppression	The alteration of a host's immune response by an infecting ***parasite***. If immune function is in some way impaired, this is termed immunosuppression.
Immunoparasitology	The study of the interaction between parasitic infection and the immune response of the ***host***.
Immunosenescence	The loss in ***immune*** function as the individual ages.
Infection	The presence of a ***parasite*** within a ***host***.
Infection intensity	Number of ***parasites*** in an infected ***host***.
Infectious disease	***Disease*** (pathology) caused by a ***parasite***, capable of being transmitted between ***hosts***.
Infracommunity	The collection of parasites ***coinfecting*** an individual ***host***.
Innate immunity	The non-specific (or less specific) immune response. Contrast with ***adaptive immunity***.

Integral projection (or population) models (IPMs)	A population dynamic modelling approach which links demographic rates across individuals to population dynamics.
Interactionist parasite communities	Within-***host parasite*** communities which are structured by interactions between ***coinfecting*** parasites. Contrast with ***isolationist parasite communities***.
Intraguild predation (IGP)	Predation among competitors within a trophic level.
Invasive alien species (IAS)	Species that have been introduced and established outside their native range.
Inverse gene-for-gene model of host–parasite compatibility	Genetic model of ***host–parasite*** compatibility in which there is a universally ***resistant*** host genotype that experiences reduced ***infection*** rates for all parasite genotypes. Contrast with ***gene-for-gene, matching alleles*** and ***inverse matching alleles models of host–parasite compatibility***.
Inverse matching alleles model of host–parasite compatibility	Genetic model of ***host–parasite*** compatibility by which a host must genetically match its parasite at relevant loci in order to ***resist infection***. Contrast with ***gene-for-gene, inverse gene-for-gene*** and ***matching alleles models of host–parasite compatibility***.
Isolationist parasite communities	Within-***host parasite*** communities in which interactions between ***coinfecting parasites*** are rare, there are many vacant niches, and species infect largely independently of each other. Contrast with ***interactionist parasite communities***.
Iteroparous	An organism which reproduces multiple times in its life. Contrast with ***semelparous***.
Koch's postulates	Criteria established by Robert Koch to identify the causative (***aetiological***) agent of a ***disease***.
Latent period	The time between an individual becoming infected with a ***parasite***, and it becoming infectious to other individuals.

Macroparasite	***Parasites*** which do not multiply inside individual ***hosts*** (e.g. helminths, ectoparasites); typically the ***parasite*** is the unit of study (e.g. the number of infecting worms). Contrast with ***microparasite***.
Major Histocompatibility Complex (MHC)	A cluster of genes that code for cell-surface proteins, which are used by the ***adaptive immune response*** to recognise specific ***antigens***.
Mass action transmission	The assumption that susceptible and infectious individuals contact each other, and therefore transmit infections, randomly.
Matching alleles model of host–parasite compatibility	Genetic model of ***host–parasite*** compatibility by which a ***parasite*** must genetically match its ***host*** at relevant loci in order to infect. Contrast with ***gene-for-gene, inverse gene-for-gene*** and ***inverse matching alleles models of host–parasite compatibility***.
Mean field approximation	The approximation of a large number of individual effects by a single averaged effect. This approximation is commonly used in ***compartmental models*** of disease spread (see ***SIR***, etc.).
Metapopulation	A collection of discrete populations in isolated patches, connected by occasional dispersal events.
Microbiota	The community of microorganisms associated with individual ***hosts***.
Microparasite	***Parasites*** which multiply inside individual ***hosts*** (e.g. viruses, bacteria, protozoa); typically the ***host*** is the unit of study (e.g. the number or proportion of infected ***hosts***). Contrast with ***macroparasite***.
Migratory allopatry	The spatial separation of adults and juveniles after breeding, which can reduce infection risk from adults to vulnerable juveniles.

Migratory culling	Mortality of infected ***hosts*** during long-distance movement events.
Migratory escape	Migration of ***hosts*** from ***parasite***-contaminated areas, thereby lowering their risk of ***infection***.
Mixing matrix	Mathematical matrix that defines the contact patterns of individuals from one population group with individuals of another group.
Muller's ratchet	The accumulation of deleterious mutations in clonal (asexual) lineages.
Negative binomial distribution	Discrete statistical distribution often used to describe the typically observed ***aggregated*** distribution of ***macroparasite*** burdens across the ***host*** population.
Network-based models	Models that include explicit contact network structure between individuals (see ***contact network***).
Ordinary infectious disease (OID)	A ***parasite*** where the majority of transmission infection occurs infectiously outside of mating contact. Contrast with ***sexually transmitted infection (STI)***.
Oxidation Handicap Hypothesis (OHH)	An extension of the ***Immunocompetence Handicap Hypothesis*** of sexual signalling, which argues that the main cost of elevated testosterone is increased oxidative stress.
Pair approximation	***Deterministic*** model approximating the dynamics of pairs of individuals in a network (see ***contact network***), rather than the dynamics of individuals themselves.
Pandemic	An **epidemic** of ***infectious disease*** that has spread across a large region, such as multiple continents or globally.
Parasite	An organism that lives in (***endoparasite***) or on (ectoparasite) another organism (the ***host***), and obtains resources from it.
Pathogen	***Parasites*** that typically cause acute, highly pathogenic ***infections***, often used as a synonym for ***microparasite***.

Pathosystem	Part of an ecosystem that involves ***parasitism***.
Phenology	The pattern and timing of life-history events such as of birth, maturation, reproduction, and death through the year.
Phyllosphere	The above-ground elements of plants, particularly in terms of the microbes associated with it.
Polygyny/polyandry	Where a single male mates with more than one female, and where a single female mates with more than one male, respectively.
Population Viability Analysis (PVA)	An analytical tool that seeks to predict the viability and extinction risk of a population.
Prevalence	The proportion of infected individuals in the ***host*** population.
Regulation (of host population dynamics)	The limitation of (***host***) population size through density-dependent feedback processes.
Reservoir (environmental)	The persistence of ***parasite*** infective stages in the abiotic environment, acting as a potential source of new ***infections***.
Reservoir (host)	A ***host*** species, or collection of species, that maintains a ***parasite*** and acts as a source of infection to another ***host*** species.
Resistance	The ability of ***hosts*** to prevent an ***infection*** from establishing or to limit its growth rate. Contrast with ***tolerance***.
Semelparous	An organism that reproduces once in its life. Contrast with ***iteroparous***.
Sexually transmitted infection (STI)	A ***parasite*** transmitted during its ***host***'s mating activity. Contrast with ***ordinary infectious disease (OID)***.
SIR, SEIR, SIS, etc. models	***Compartmental models*** of ***microparasite*** dynamics, structured according to assumptions about the flow of ***host*** individuals between compartments defined by their ***infection*** status ***(S=susceptible*** (uninfected), *I*=infected (and infectious), *E*=exposed (infected but

	not infectious), *R*=recovered (and immune from reinfection)).
Social immunity	Collective ***host*** behaviours that reduce the likelihood of ***infection*** in social or communal species.
Spillover	The process by which ***parasites*** from one host species (typically a ***reservoir host***) cross over to infect a different ***host*** species.
Stochastic	A system or modelling framework which incorporates some element of random variation. Contrast with ***deterministic***.
Subclinical infections	Infections which result in no obvious signs of ***disease*** in the ***host***.
Supershedder	Individuals that are highly infectious through high levels of release of ***parasite*** infective stages. See also ***superspreader***.
Superspreader	An individual ***host*** that contributes disproportionately highly to parasite transmission (e.g. due to their high number of contacts with other individuals). See also ***supershedder***.
Susceptible [host]	A ***host*** that can be infected by a specific ***parasite***.
Th1/Th2 immune response	Characterisation of the immune response into the 'T-helper 1' (Th1) and 'T-helper 2' (Th2) arms, based on the different ***cytokines*** and ***antibodies*** produced, typically in response to intracellular (~***microparasitic***) or extracellular (~***macroparasitic***) infections, respectively. Often these arms of the ***immune response*** are assumed to trade-off against each other, such that investment in one response limits the ability of the ***host*** to invest in the other.
Threshold population size/critical community size	The minimum ***host*** population size required for a ***parasite*** to persist.
Tolerance	The ability of ***hosts*** to reduce the detrimental impact of a given ***infection***. Contrast with ***resistance***.

Trait-mediated effects (of parasitism)	***Infection*** alters ***host*** traits such as appearance or behaviour, which affects vulnerability to predation, potentially affecting population, community, or ecosystem dynamics.
Trait-mediated indirect effects (TMIE) (predator-mediated)	Indirect effects on a ***host–parasite*** interaction, mediated by another member of the community. May be predator-mediated (e.g. non-lethal effects of natural enemies on ***hosts***, which alter traits such as ***host*** behaviour, rather than survival) or resource plant) mediated (e.g. plant traits affect the interaction between herbivores and their natural enemies).
Transmission	The process by which a ***susceptible*** (uninfected) ***host*** acquires a new ***infection***.
Trickle infection	Experimentally infecting ***hosts*** with low, repeated doses of ***parasites***, to mimic the natural rate of acquisition of ***infections***.
Trophic cascade	Changes in the structure of a community occurring when predators reduce the density of their prey, which has knock-on effects at lower trophic levels.
Trophic transmission	The ***transmission*** of ***parasites*** between trophic levels through the ingestion of infected prey by predators, which then become infected.
Vertical transmission	***Transmission*** directly from parent to offspring, for example trans-placental (in mammals) or via eggs (e.g. in insects). Contrast with ***horizontal transmission***.
Virulence	The impact of a ***parasite*** on its ***host's*** fitness (i.e. through reduction in individual ***host*** survival or reproduction). See also ***virulence (density-dependent)***.
Virulence (density-dependent)	***Host*** fitness cost of ***infection*** (***virulence***) increases as host density increases.
Zoonosis	An ***infectious disease*** that is maintained in a wild ***reservoir***, but which may cause ***infection*** in humans.