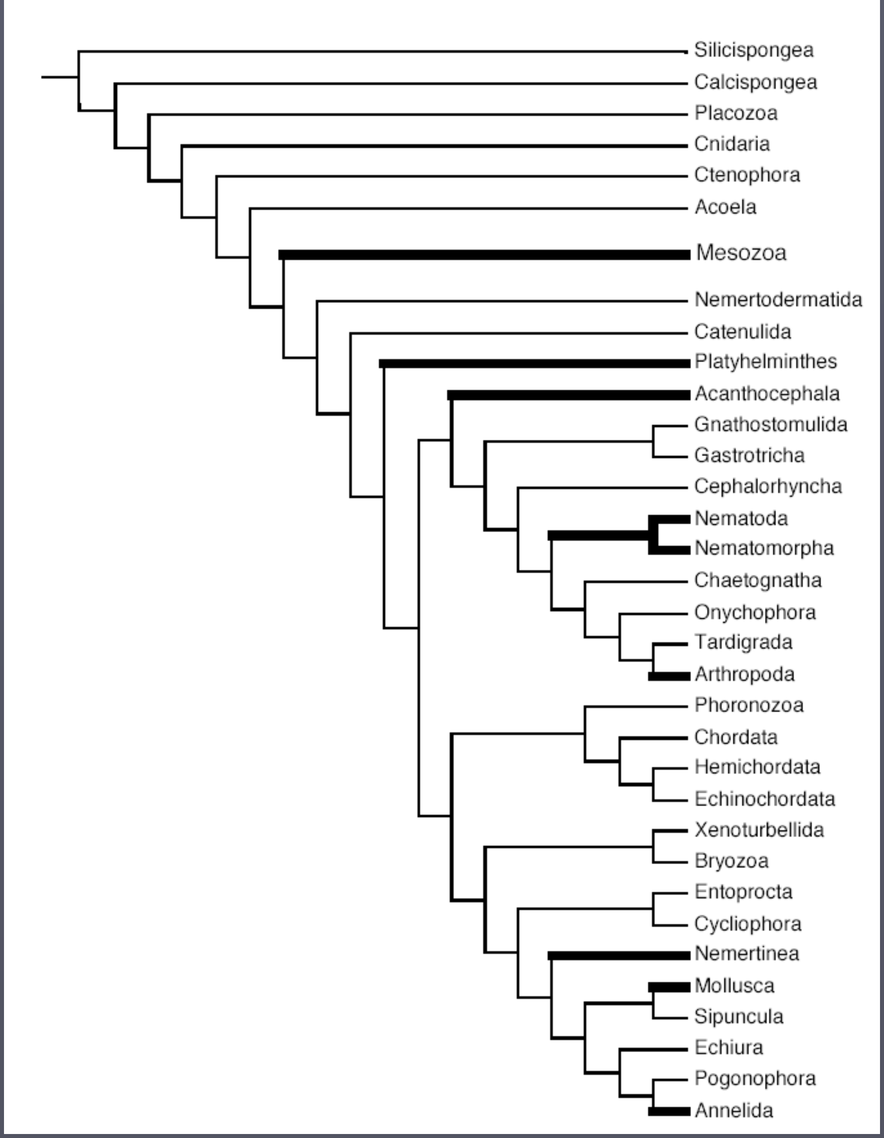
Parasite diversity

Parasite diversity

1 000 000 described species of eukaryotes
100 000 described species of parasites



(Poulin & Morand, 2004)

Parasite diversity

> 70 transitions from free-living strategy to parasitic life strategy

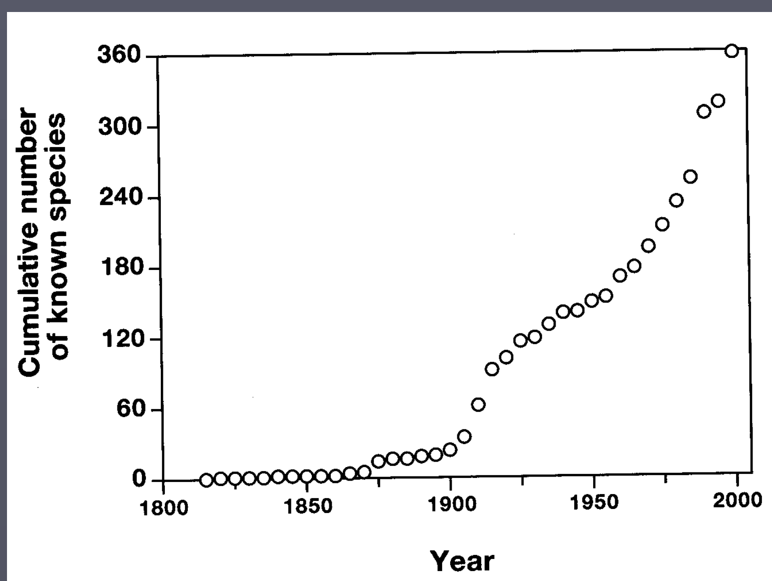
Parasite Taxon	Minimum Numbers of Transitions	Minimum Numbers of Living Species	Source
Phylum Mesozoa	1	>80	Barnes 1998
Phylum Myxozoa	1	>1,350	Okamura and Canning 2003
Phylum Platyhelminthes*			
Class Cercomeridea (subclasses Trematoda, Monogenea, Cestoidea)	1	>40,000	Brooks and McLennan 1993a; Rohde 1996
Phylum Nemertinea*	1	>10	Barnes 1998
Phylum Acanthocephala	1	>1,200	Amin 1987
Phylum Nematomorpha	1	>350	Schmidt-Rhaesa 1997
Phylum Nematoda*	4	>10,500	Blaxter et al. 1998; Anderson 2000
Phylum Mollusca*			
Class Bivalvia*	1	>600	Davis and Fuller 1981
Class Gastropoda*	8	>5,000	Warén 1984
Phylum Annelida*			
Class Hirudinea*	3	>400	Siddall and Burreson 1998
Class Polychaeta*	1	>20	Hernández-Alcántara and Solis-Weiss 1998
Phylum Pentastomida	1	>100	Barnes 1998
Phylum Arthropoda*			
Subphylum Chelicerata*			
Class Arachnida*			
Subclass Ixodida	1	>800	Klompen et al. 1996
Subclass Acari*	2	>30,000	Houck 1994
Subphylum Crustacea*			
Class Branchiura	1	>150	Barnes 1998
Class Copepoda*	9	>4,000	Humes 1994; Poulin 1995a
Class Cirripedia*			
Subclass Ascothoracida	1	>100	Grygier 1987
Subclass Rhizocephala	1	>260	Høeg 1995
Class Malacostraca*			
Order Isopoda*	4	>600	Brusca and Wilson 1991; Poulin 1995b
Order Amphipoda*	17	>250	Kim and Kim 1993; Poulin and Hamilton 1995
Subphylum Uniramia*			
Class Insecta*			
Order Diptera*	2	>2,300	Price 1980
Order Phthiraptera (suborders Ischnocera, Amblycera, Anoplura)	1	>3,000	Barker 1994
Order Siphonaptera	1	>2,500	Roberts and Janovy 1996

* Taxon also contains free-living species.

(Poulin & Morand, 2004)

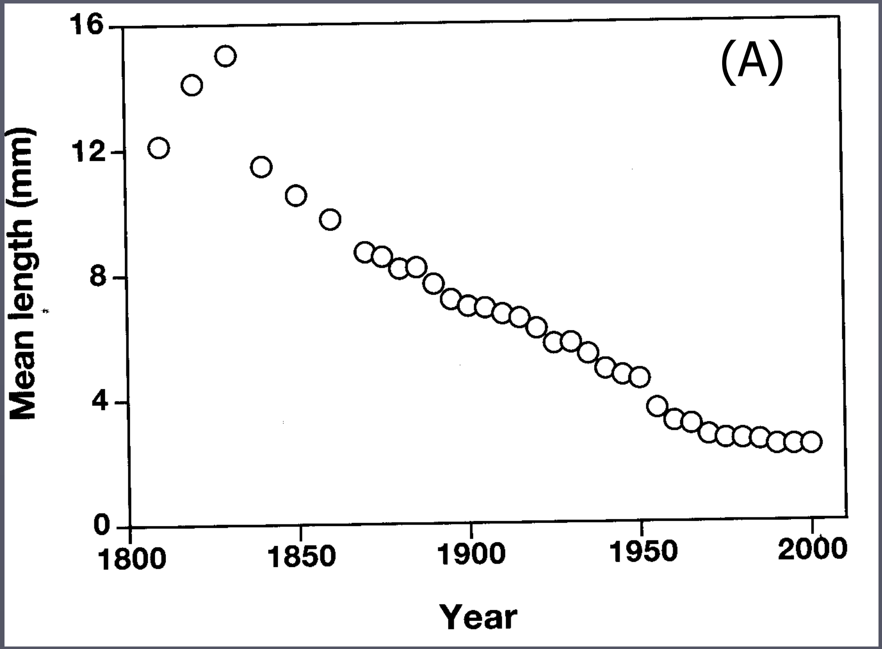
Parasite diversity

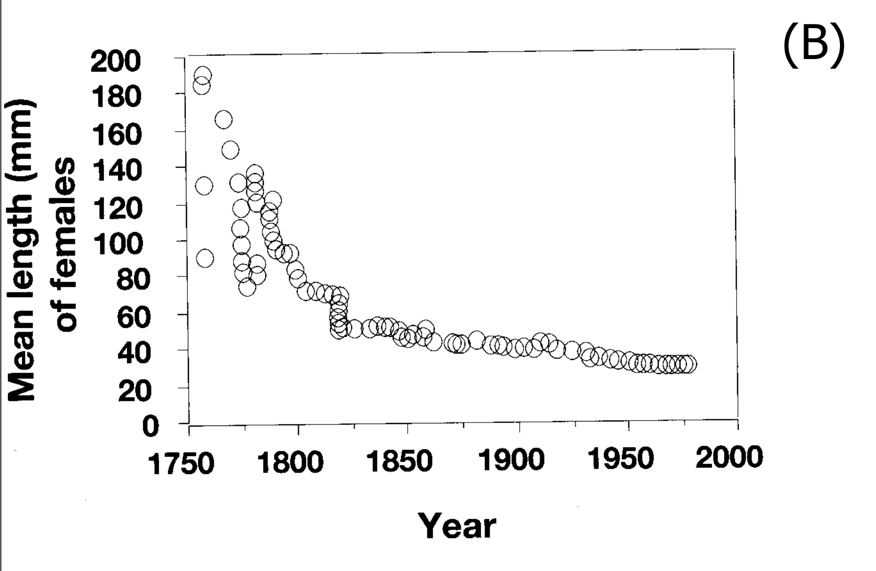
- What are our knowledge?
- Rate of description of new species as an indicator of diversity (in a given geographical area)
- Ex. Cumulative number of Cestoda species from vertebrates of Australia over time



Many parasites are waiting to be discovered and described

Parasite diversity





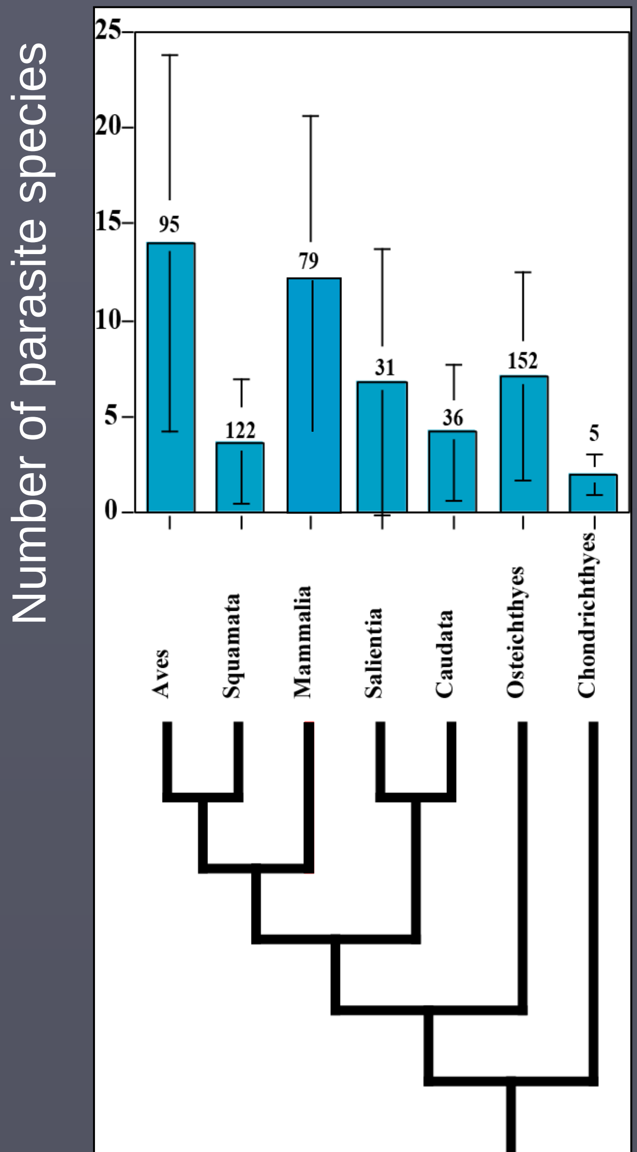
Ex. Average body size of monogeneans (A) and female nematodes parasitizing vertebrate animals (B) decreases over time with increasing number of species discovered

Parasite diversity

Mammals and birds have a high number of species of parasites

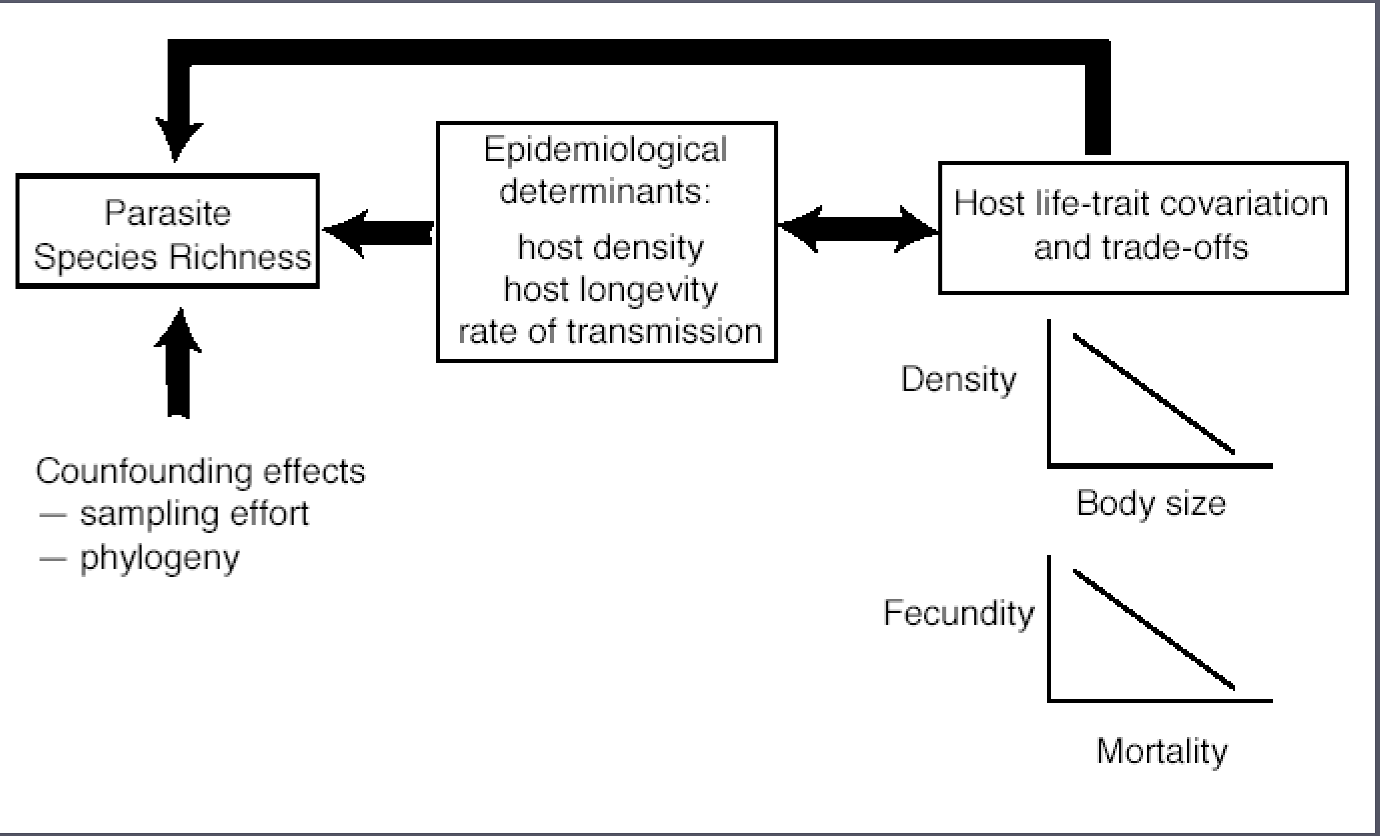
At all levels from the host's point of view:
- Host individual (infracommunity)
- Host population (metacommunity)
- Host species (parasitofauna)

At all levels of the geographical scale:
- local, regional, global



(Combes & Morand, 1999)

Determinants of parasite diversity

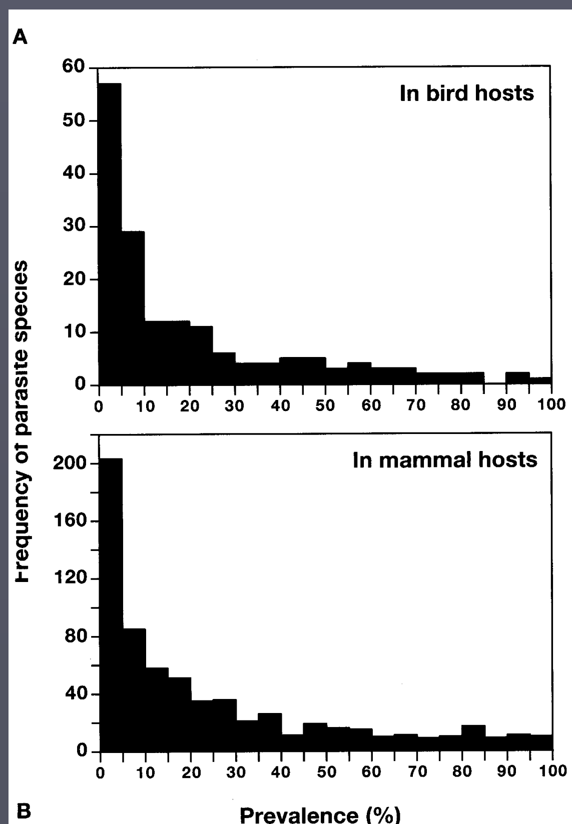


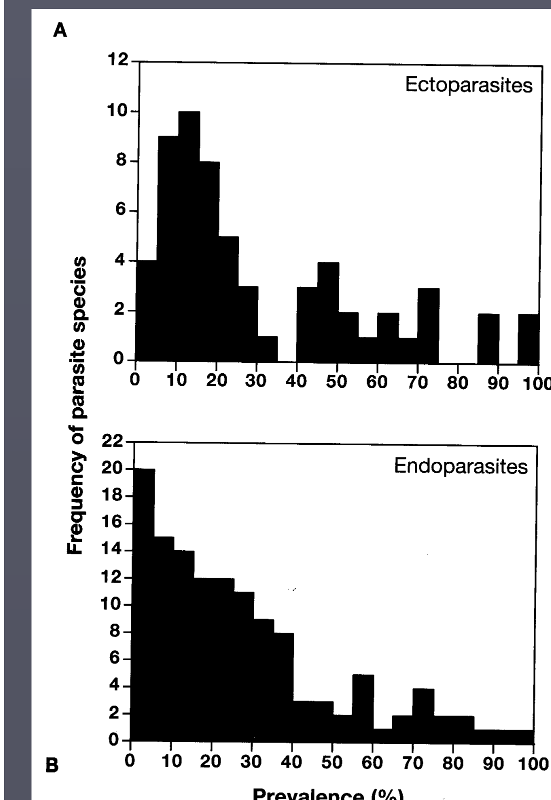
Effect of sample size on estimation of parasite diversity

- Many parasites are not detected in the host sample studied due to their low prevalence
- Ex. Prevalence of parasites in birds and mammals ≤ 5%, in fish <20%

167 species og gastrointestinal helminths from 20 metacommunities

644 species of helminths from 77 metacommunities



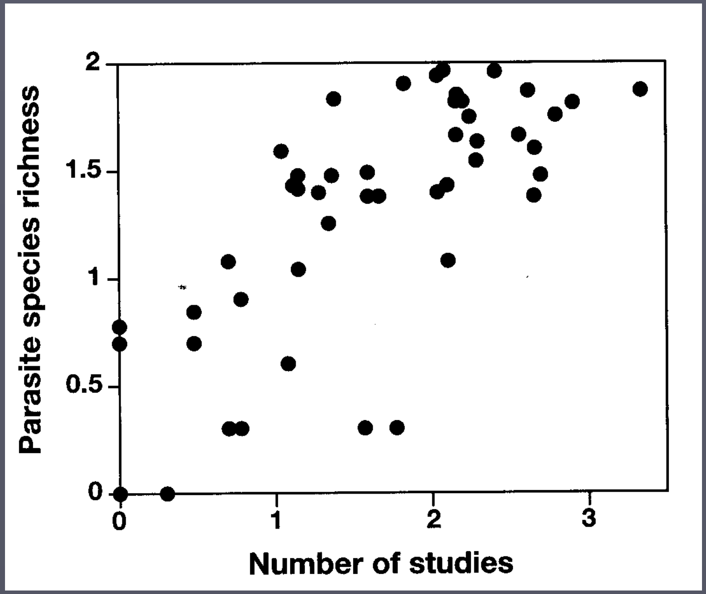


60 species of metazoan ectoparasites

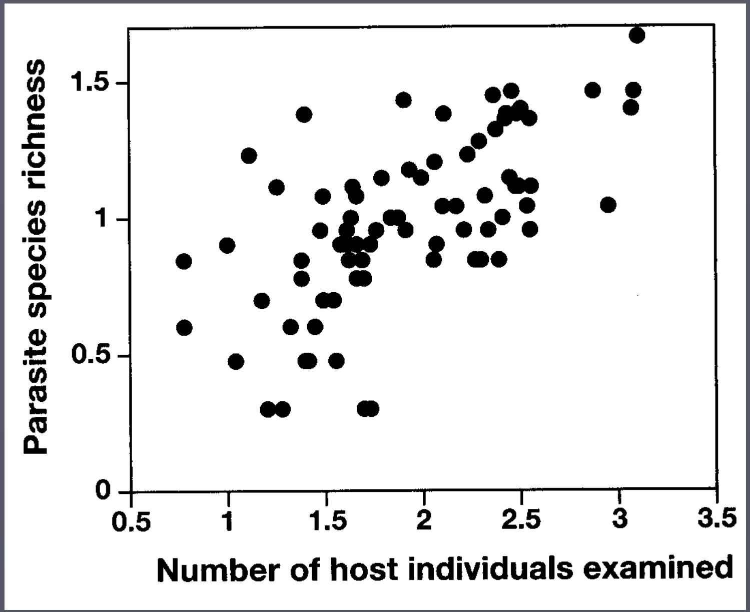
128 species of gastrointestinal helminths

both from 88 metacommunities of freshwater fish

Effect of sample size on estimation of parasite diversity

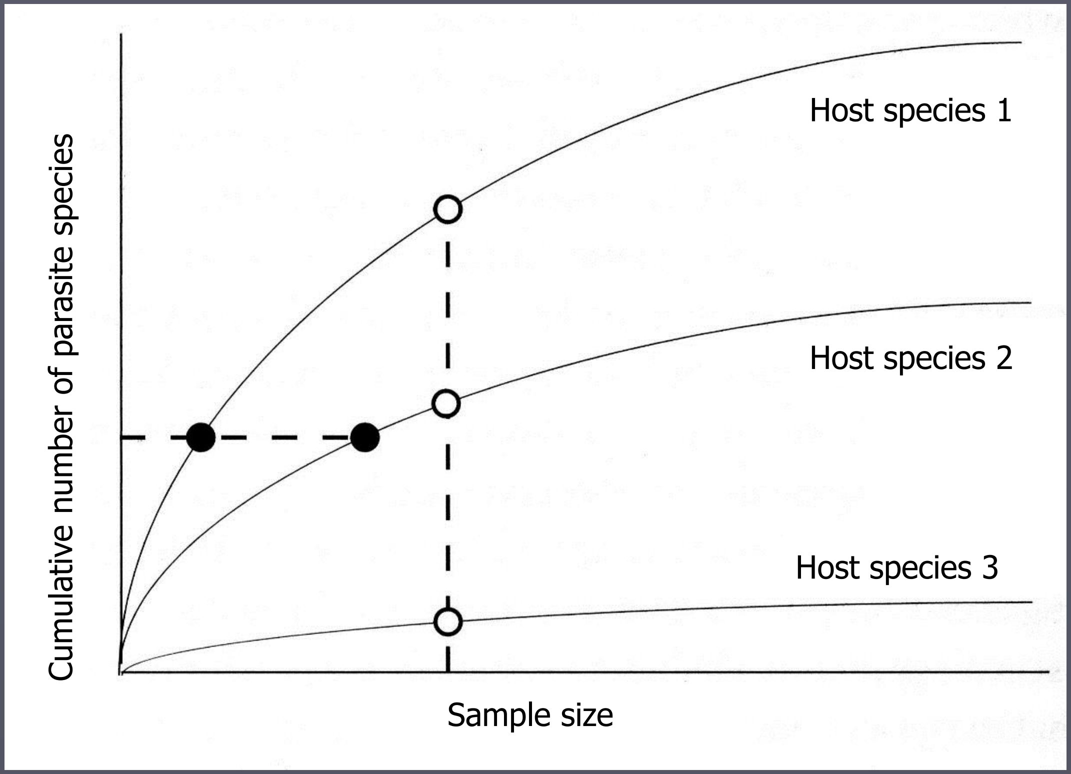


Number of metazoan parasite species versus the number of studies per host species during 10 years
49 freshwater fish species of North America



Number of gastrointestinal helminth species versus the number of examined host individuals in 79 mammalian species

Effect of sample size on estimation of parasite diversity



Correction for sample size

- Use of residues
- - residues of the number of parasite species (i.e. the number of parasite species is corrected for the size of the host sample (Gregory, 1990))

- Use of estimators of the number of parasite species
  - individual data (Walther & Morand, 1997, Poulin 1998)
  - 3 non-parametric methods (or their modifications) for estimating the number of species:
    Jacknife estimator, Chao estimator, bootstrap estimator

Estimators of the number of parasite species

$S_{jack1} = S_{obs} + Q_j(m\text{-}1/m)$

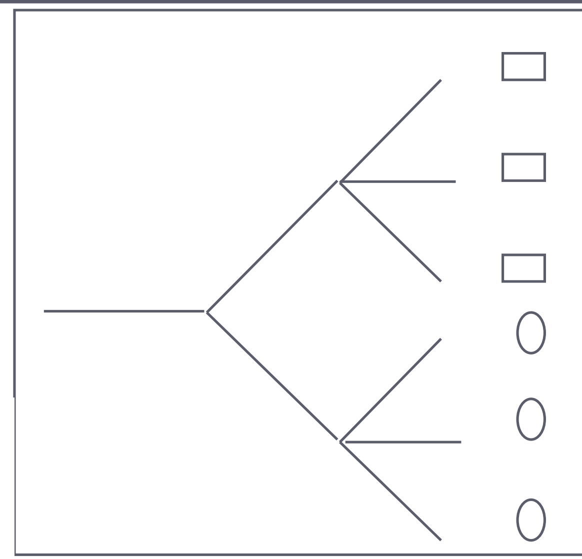
where S_{obs} is the total number of parasite species recorded on all examined hosts, Qj is the number of parasite species occurring on the number j of randomly selected individuals and m is the total number of sampled hosts

$$S_b = S_0 + \sum_{j=1} S_o[1\text{-}(h_j/H)]H$$

where S_0 is the number of species observed, i.e. the number of species currently present in the sample, H is the number of host individuals in the sample, hj is the number of host individuals on which the parasite species j was found

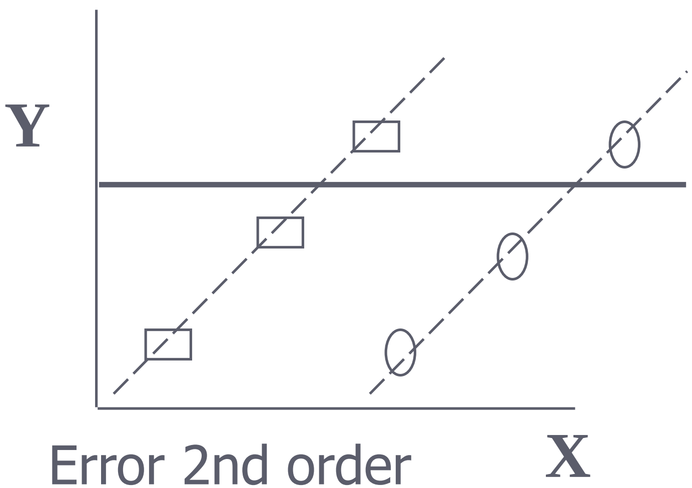
Effect of host phylogeny on parasite diversity

H_O – no relationship between X and Y

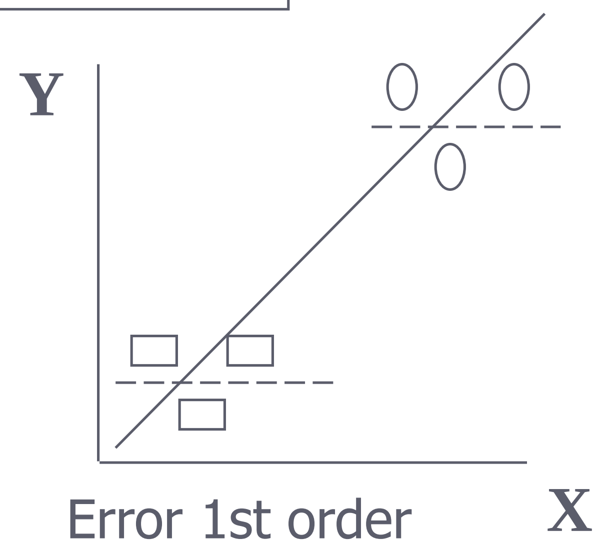


Wrong acceptence of H_O

Wrong rejection of H_O



Error 2nd order

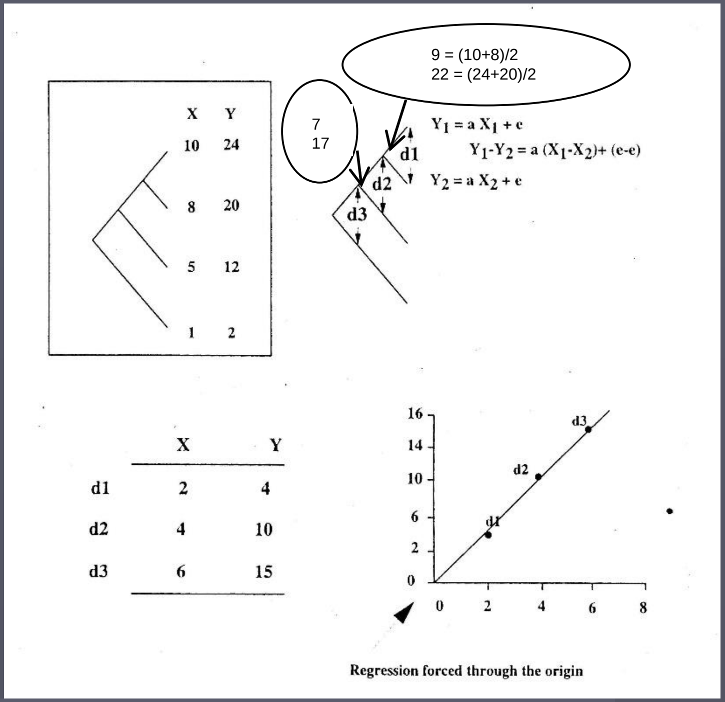


Error 1st order

Method of phylogenetically independent contrasts

(1) Independent contrasts compare values corresponding to sister taxa

(2) Calculation of values for a common ancestor

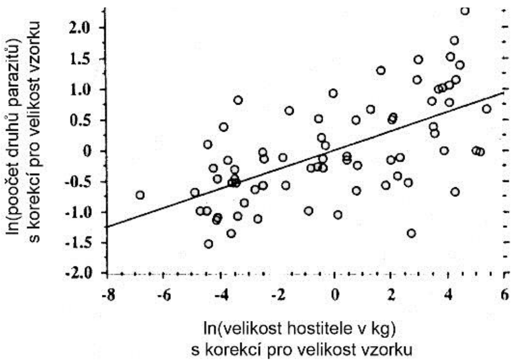


(3) Three independent contrasts (d1, d2, d3) were obtained by calculation
Ex. calculation d1(X) = 10-8, d1(Y) = 24-20, d2(X)=9-5, d2(Y)=22-12

(4) The regression line passes through 0

Method of phylogenetically independent contrasts

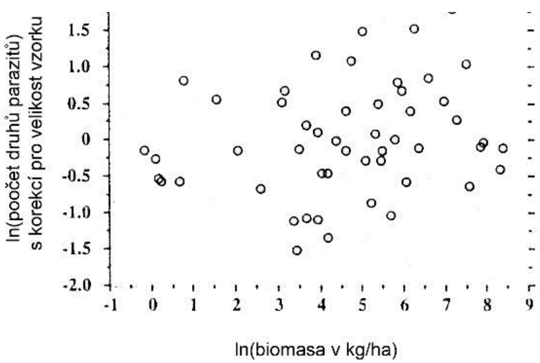
Interspecies comparison without phylogenetic recontrusction



Významný ($P < 0.001$)

Chybné zamítnutí H_0
Chyba I. řádu

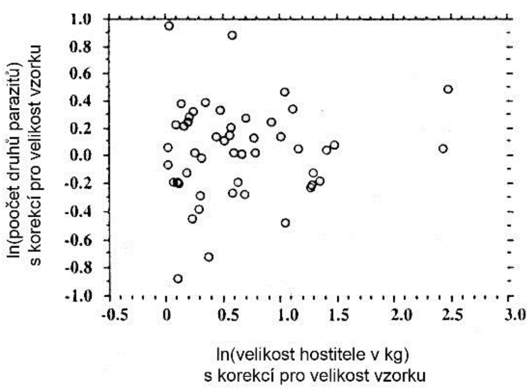
Interspecies comparison without phylogenetic recontrusction



N.S. (P=0.11)

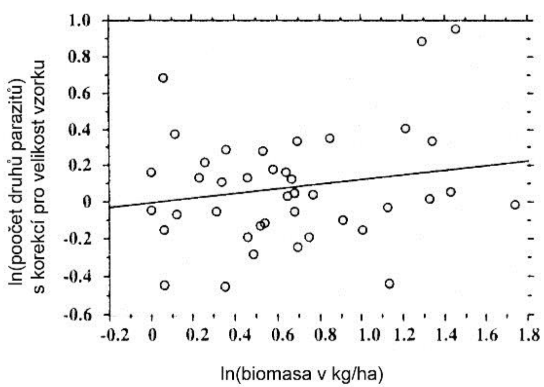
Chybné akceptování H_0
Chyba II. Řádu

Interspecies comparison with phylogenetic recontrusction



N.S. (P = 0.33)

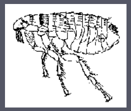
Interspecies comparison with phylogenetic recontrusction

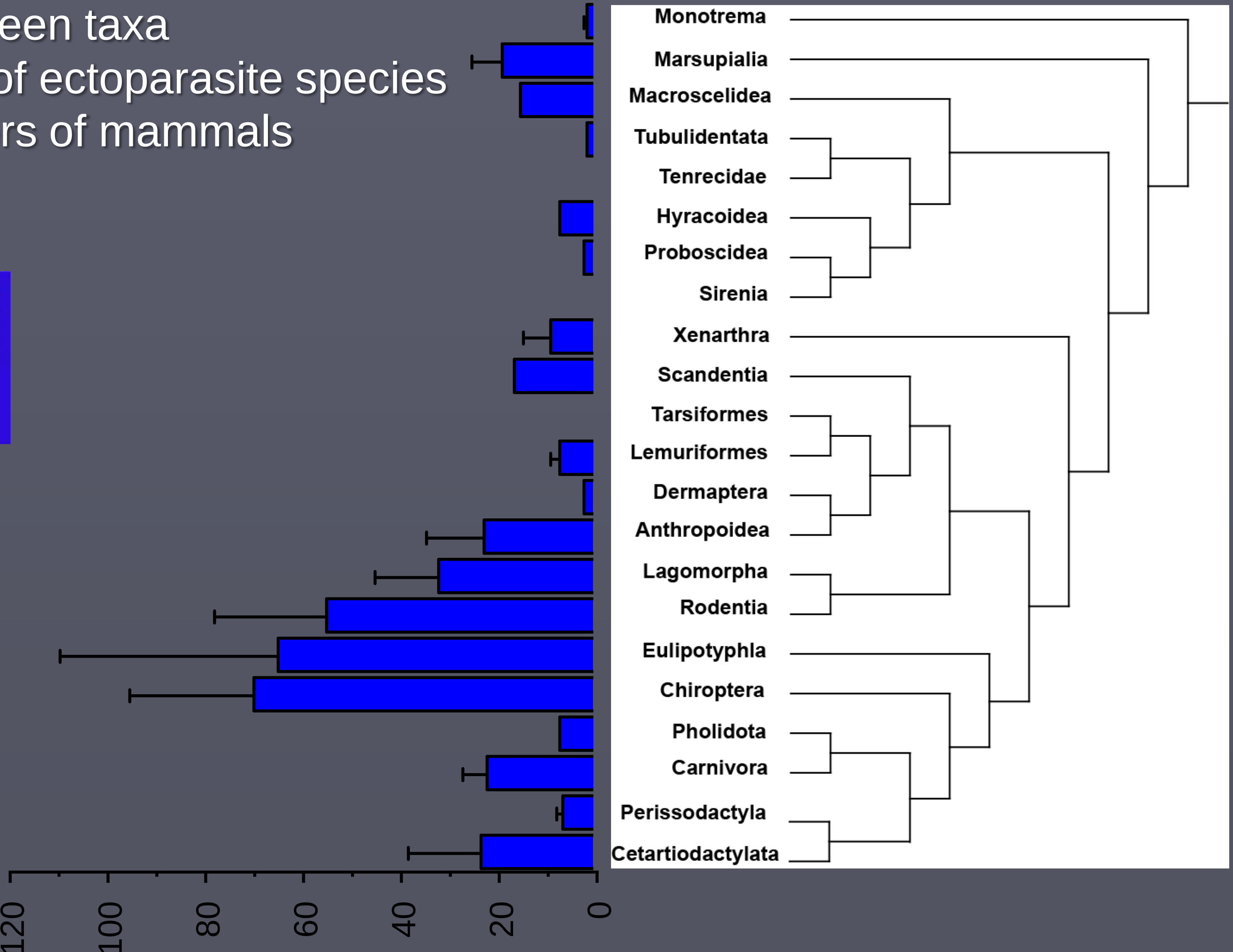


Významný (P=0.038)

Parasite diversity and host diversity

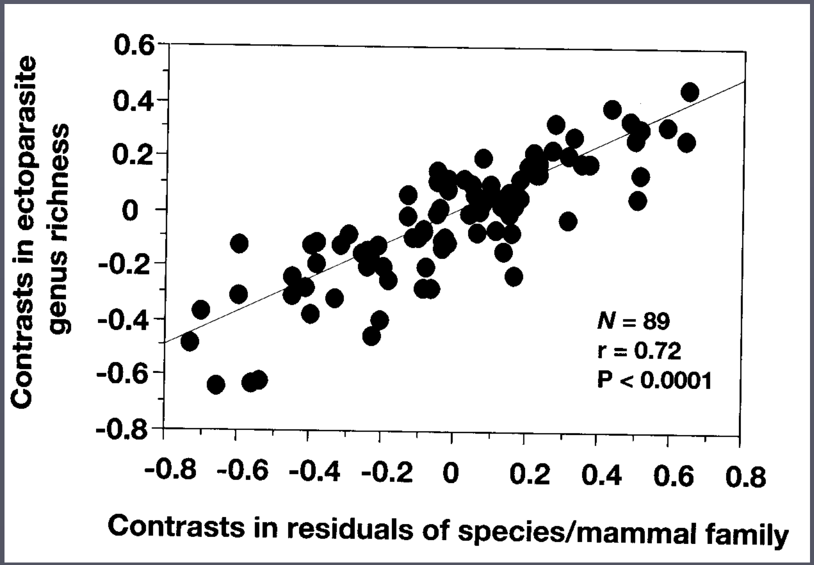
Variability in the number of ectoparasite species between taxa
e.g. number of ectoparasite species in major orders of mammals



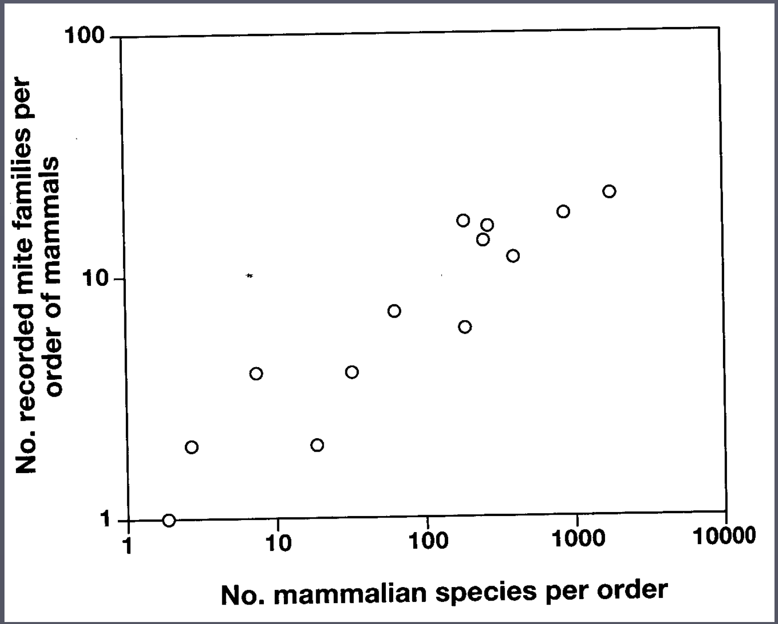


Parasite diversity and host diversity

Positive relationship between number of parasites and number of hosts - result of coevolution and codiversification (host-specific parasites)
Ex. malaria-causing parasites - *Plasmodium* and *Haemoproteus* in birds



Ex. Relationship between ectoparasie diversity (arthropods) and mammalian diversity
Corrections for phylogeny and body size

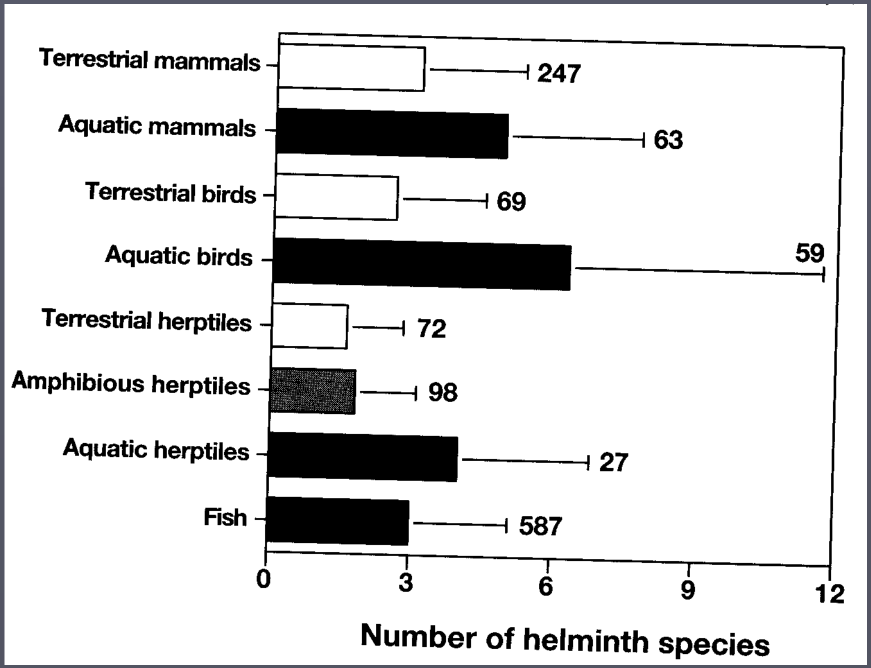


Ex. Relationship between mite diversity on host taxon and mammalian diversity (number of mammal species per order)

Parasite diversity and host habitat type

Parasites and habitat type of hosts: aquatic versus terrestrial

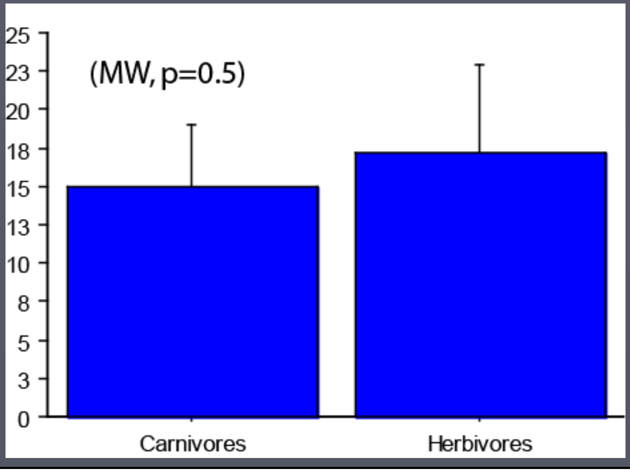
Comparison of the number of intestinal helminth species between different groups of vertebrates

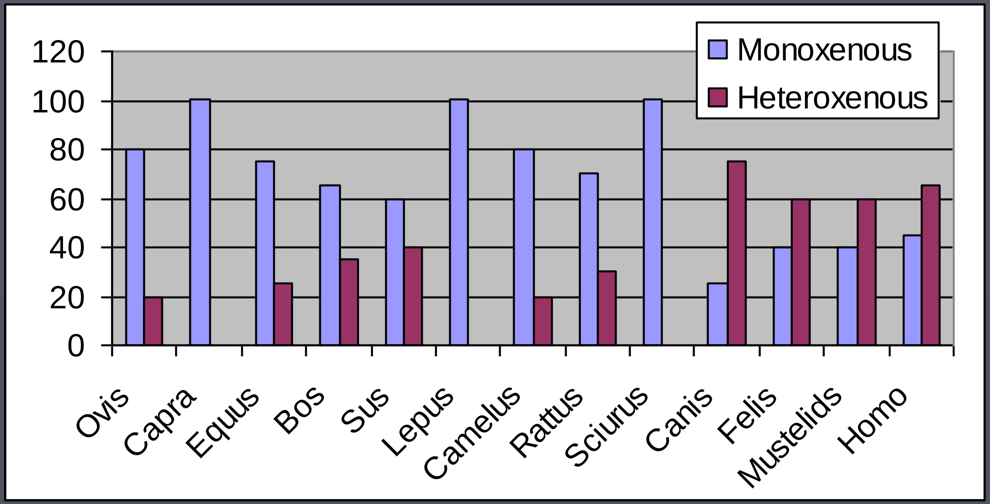


Parasite diversity and type of host food

mammals: carnivores versus herbivores

Carnivora Cetartiodactyla





Classical views on determinants of parasite diversity

1) Latitude gradient

Low latitudes lead to greater diversification

- Host species living in low latitudes (tropics) have more parasite species

2) The relationship between area size and diversity

Hosts considered islands for parasites

- Larger host species and/or host species with wider geographical distribution show higher parasite diversity

3) Theory of epidemiology (Anderson & May, 1978, 1991)

The transmission of parasites depends on the exposure of the hosts and the frequency of contacts

- higher survival, population density and size lead to higher parasite diversity

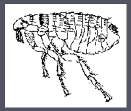
Latitude gradient of parasite diversity

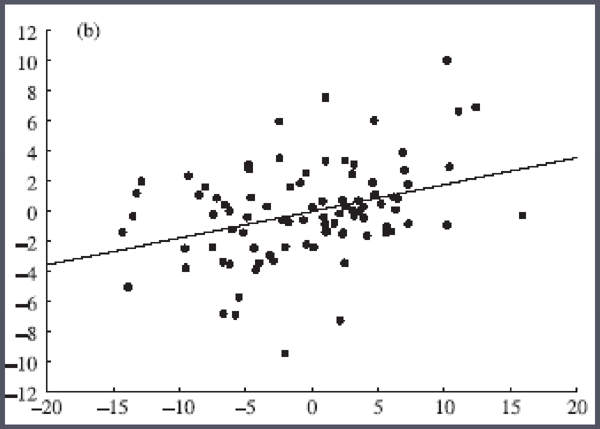
No: Mammals and helminths (Poulin, 1995)

No: Primates and helminths (Nunn et al., 2005)

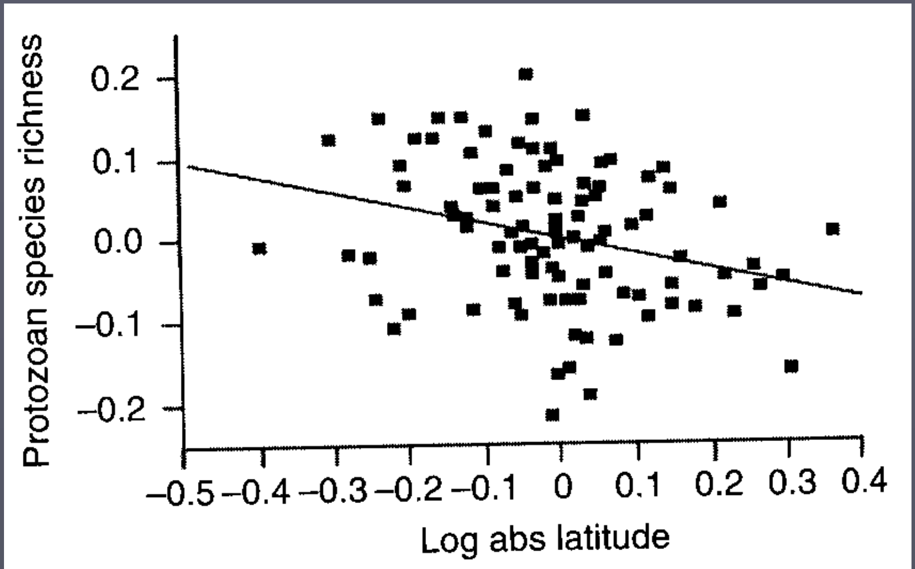
No: North American mammals and helminths (Morand, 2002)

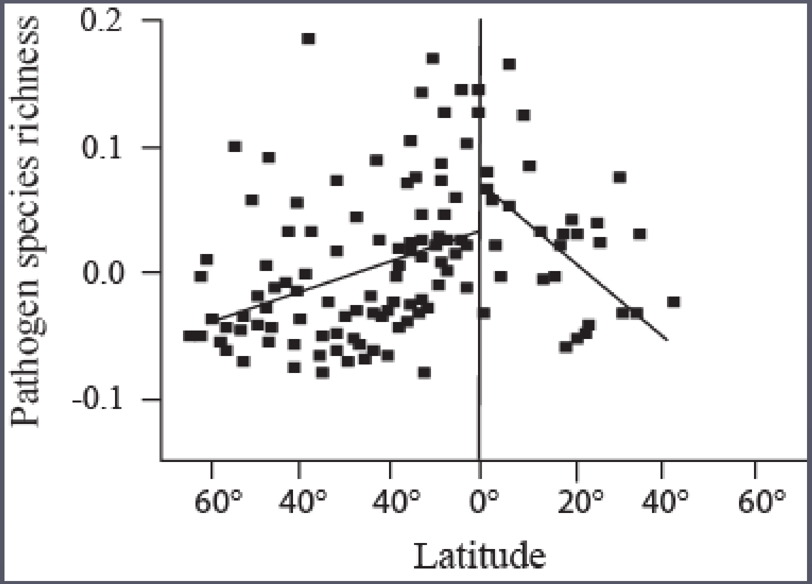
Yes: Rodents and fleas (Krasnov et al., 2004), but the opposite trend!
the effect of climatic factors within a given latitude or specific environmental factors





Latitude gradient of parasite diversity





Yes: Primates and microparasites (Nunn et al., 2005)

Yes : Humans and microparasites (Guernier et al., 2004)

Concept of area size vs. diversity

Theory of island biogeography (MacArthur & Wilson, 1967)

The number of species on the island reflects the balance between the degree of colonization and the degree of extinction of the species

- hosts = islands for parasites (Kuris et al., 1980)

Island size ~ host size

Island age ~ life expectancy of the host species or population

Distance of the island from the mainland ~ geographical distribution of hosts

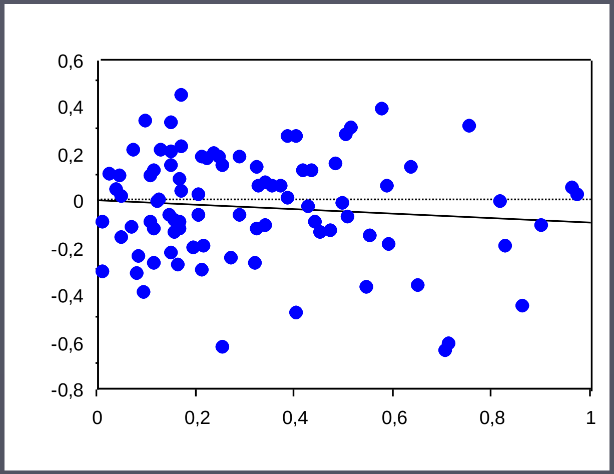
Parasite diversity and host size

- Island size = larger host (length, weight) - more space and food resources for parasites, higher diversity of microhabitats
- Positive relationship between host size (length, weight) and parasite diversity
- The need for correction for sample size and phylogenetic effects

Parasite diversity and host size

- Ex. Positive relationship between fish size and number of monogenean species in fish of the Cichlidae or African members of the Cyprinidae
- Ex. There is no relationship between the number of ecto- or endoparasites and the weight in mammals

Ectoparasite
Genera (contrasts in number)



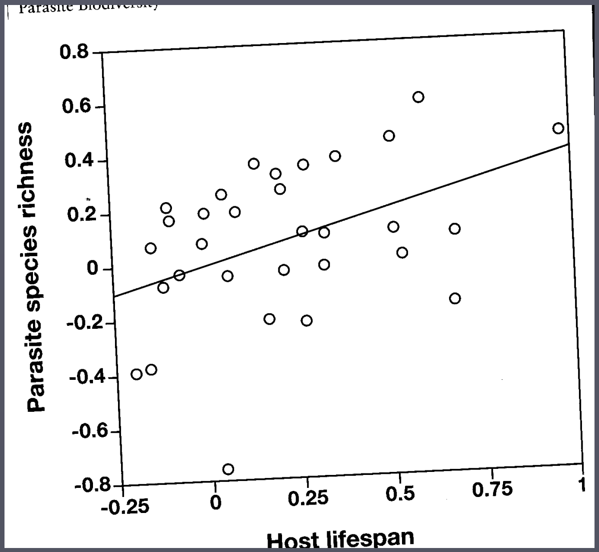
Mean Mammal Body Weight
(contrasts in Log kg)

Parasite diversity and host biomass

- Island size = host biomass per unit area
- Ex. One elephant versus very numerous rodents
- biomass = product of body weight and density

Parasite diversity and host life span

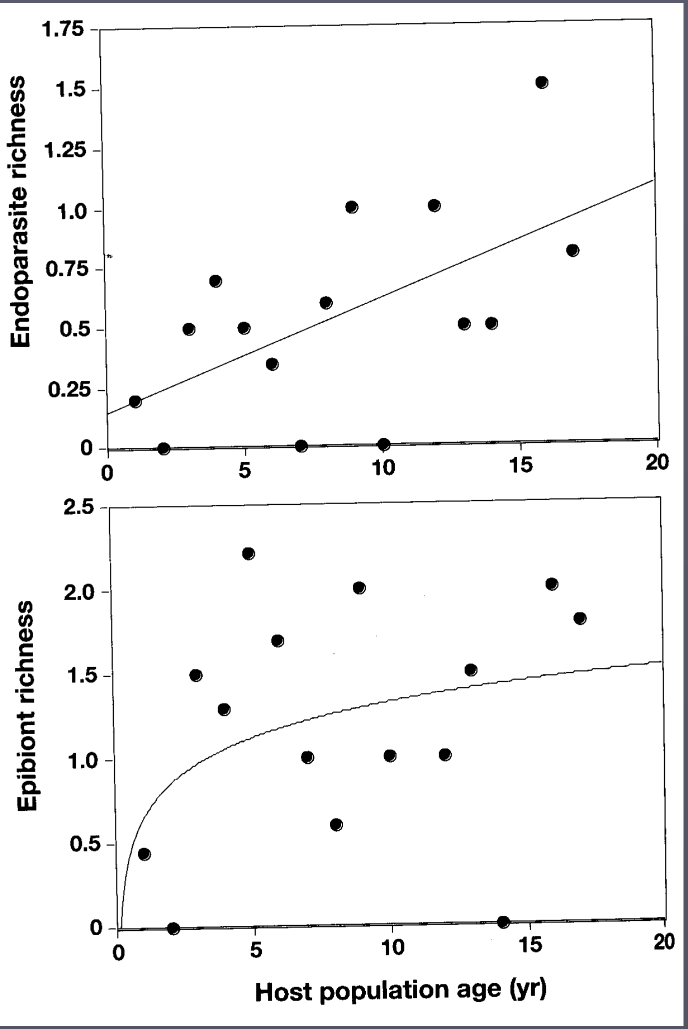
- Life expectancy of the host - effect on the degree of colonization by parasite species
- Longer-lived host species have more parasite species than short-lived hosts (empirical evidence of the relationship is limited)



Ex. Number of endoparasitic helminth species and the life expectancy of North American freshwater fish

Parasite diversity and age of the host population

- New island - without life
  ~ new host or population
  - few parasite species
    in the population of the founder
- Over time – colonization of
  new species and speciation – positive relationship between number of parasite species and age of population to the stabilization stage of the number of species

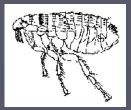


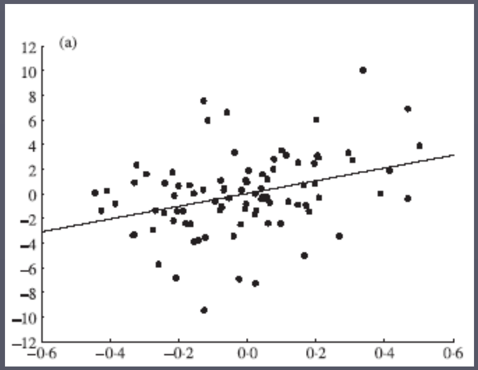
Ex. host crustacean population - *Daphnia magna*

Parasite diversity and geographical distribution of the host

Flea diversity in rodents (Krasnov et al. 2004)

The number of flea species increases with higher geographical distribution of hosts



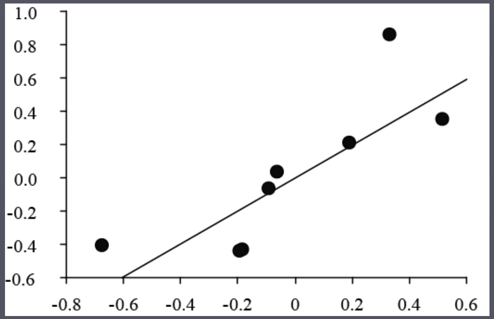


Number of species of fleas

Scope of distribution

Helminth diversity in carnivores (Torres et al., 2006)

The number of helminth species increases with higher geographical distribution of hosts



Number of helminth species

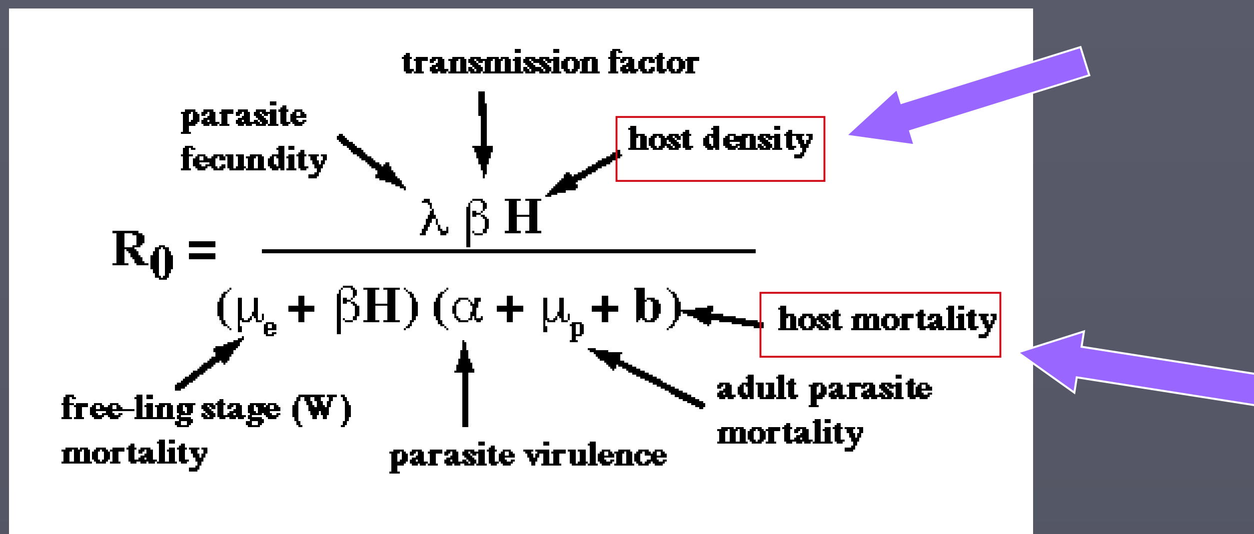
Scope of distribution

Epidemiology: parasite diversity and density of host populations

- Epidemiological determinant
- Basic reproduction rate R_0
- R_0 for microparasites - number of infections produced by the pathogen entering the susceptible host population
- R_0 for macroparasites - the average number of offspring produced during the life of a female and reaching sexual maturity under conditions of absence on density-dependent restrictions

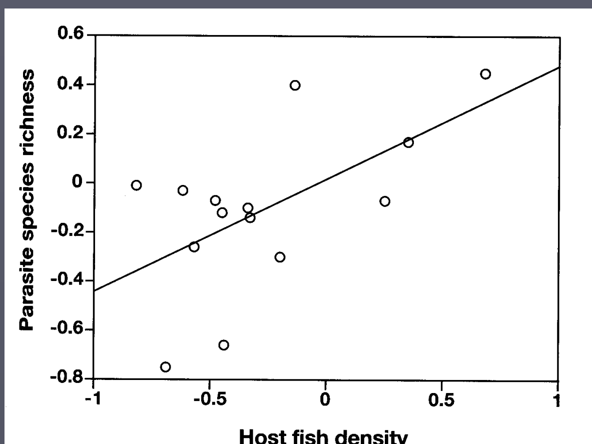
- $R_0 < 1$ - parasite tends to local extinction
- $R_0 > 1$ - the parasite successfully invades the host population, the number of parasites grows to equilibrium state

Parasite diversity and host population density

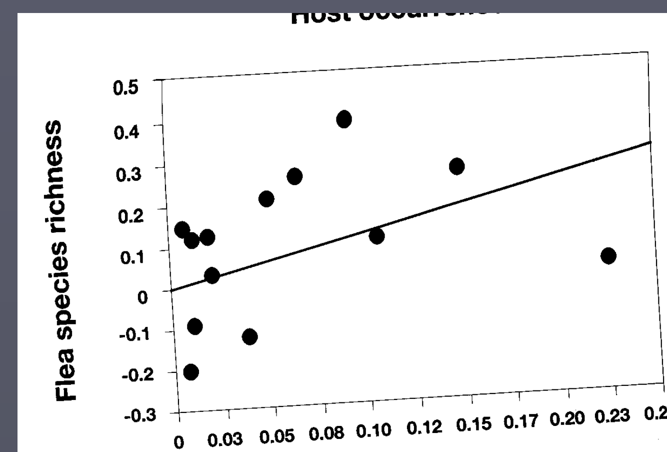


Parasite diversity and host population density

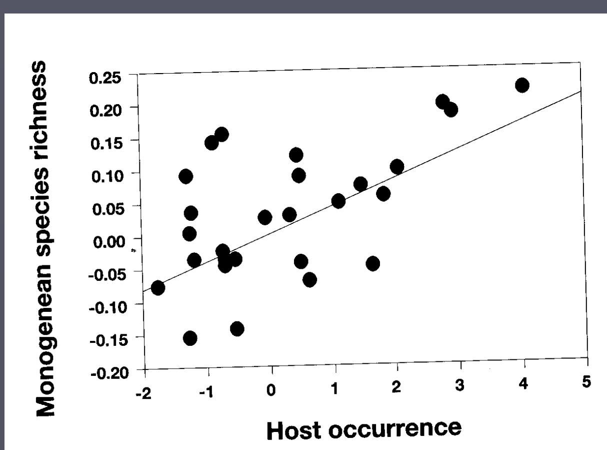
- Host density encourages the accumulation of parasite species in host populations
- A positive relationship is not always strong



Number of parasite species vs. host density in fish of the Chaetodontidae



Number of flea species vs. population density of host mammals



Number of monogenean species vs. frequency of fish occurrence (Cyprinidae)

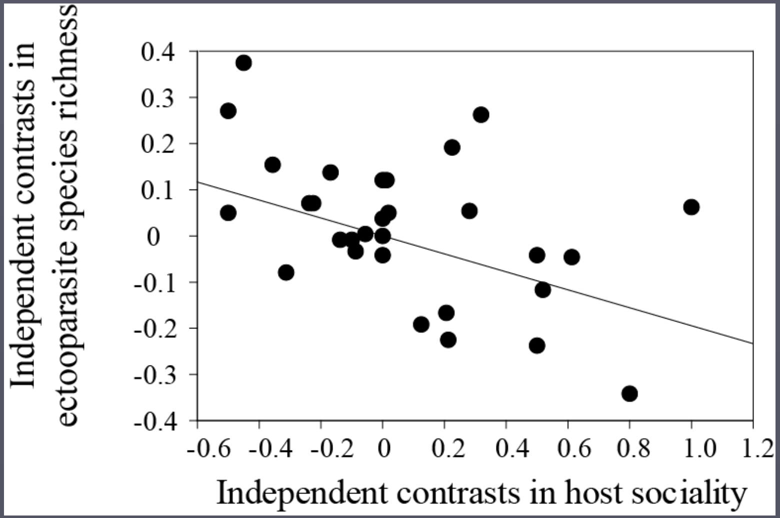
More recent perspectives on the study of determinants of parasite diversity

- Classical predictions indicate several universal rules: host density, geographical distribution
- Some studies show conflicting relationships: latitude, group size, life expectancy
- The expression of some determinants is inaccurate, e.g. the size of the group does not reflect host sociality
- Host behavior is rarely studied

- Therefore new approaches, new hypotheses

Parasite diversity and host sociality

- Sociality of rodent hosts (Bordes et al. 2007)
- Sociality index instead of using group size
- Ex. Diversity of helminths and arthropods in 46 rodent species



H1: benefits of host species living in social groups in relation to behavioral protection of allogrooming

H2: avoidance of parasites through dilution effect

Parasite diversity and host sociality

In *Rhabdomys pumilio*, the daily energy expenditure is lower in larger ones groups (Scantlebury et al. 2006)
probably less energy costs for thermoregulation
stored energy used for costly immunity?

Parasite diversity and home range

- Home range

The infectious stages of macroparasites are highly aggregated and immobile

The home district of hosts is a potential determinant of parasite contacts - it affects the parasite diversity

- From the point of view of the hypothesis for area size versus parasite diversity

a larger home district provides more opportunities for parasite contacts and accumulation of higher parasite diversity

(Nunn et al. 2003; Ezenwa et al. 2006; Lindenfors et al. 2007)

Parasite diversity and home range

- Based on epidemiology, the opposite prediction

Great home district

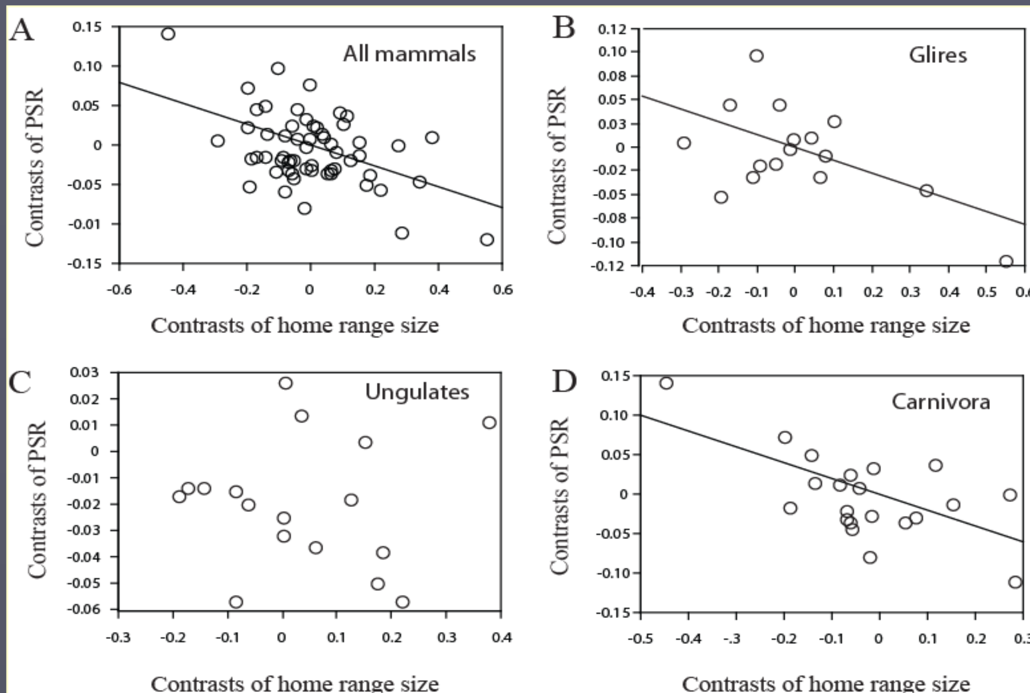
Low density host

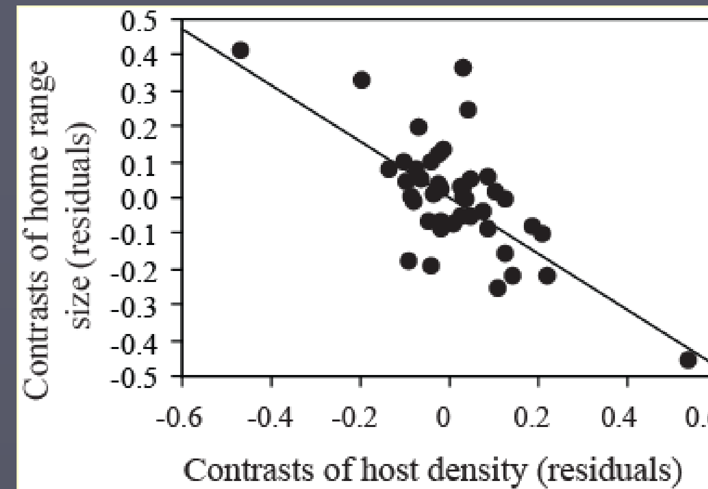
Aggregated distribution of larval stages

Low transmission parasites

Reduced parasite diversity

Parasite diversity and home range





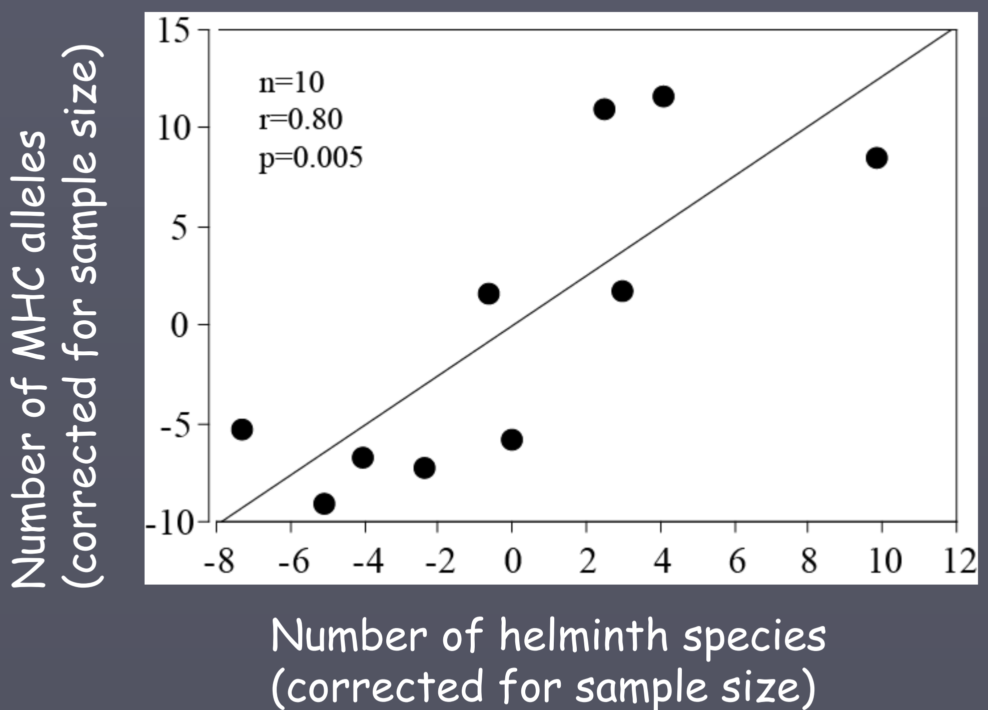
Negative relationship between the size of the home district and the number of parasite species in mammals in accordance with the epidemiological assumption

Negative relationship between host density and home district size

Bordes et al. 2009

Diversity of parasites and diversity of host immune genes

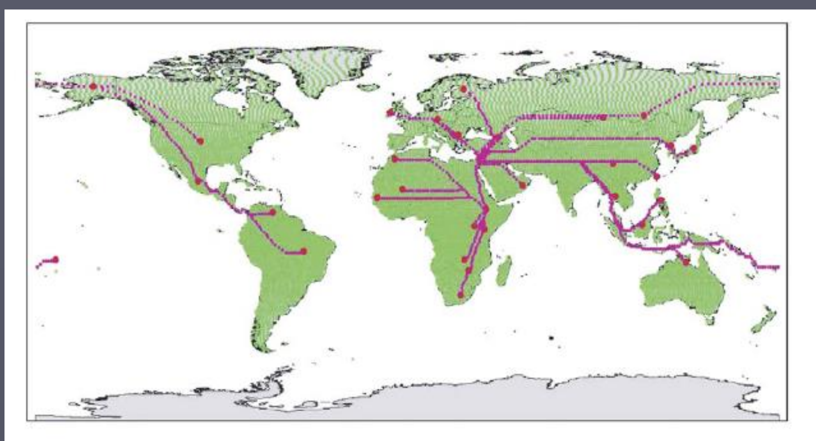
High parasite diversity maintains high genetic diversity of hosts
Immune genes (MHC, major histocompatibility complex)

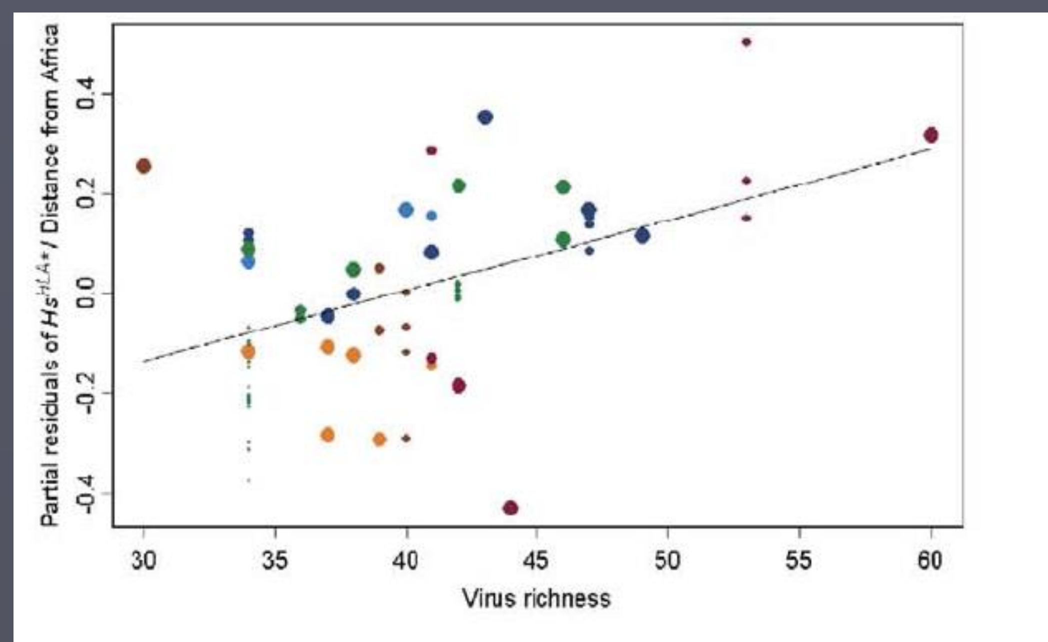


(Goüy de Bellocq et al. 2007)

Diversity of parasites and diversity of host immune genes

Pathogen-Driven Selection and Worldwide HLA Class I Diversity

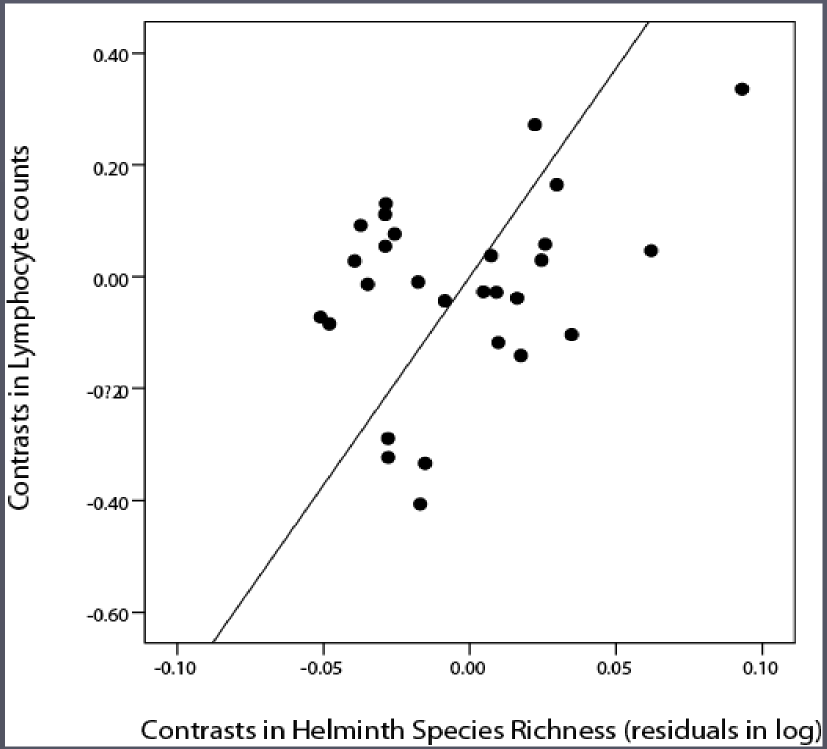




(Prugnole et al., Current Biology 2005)

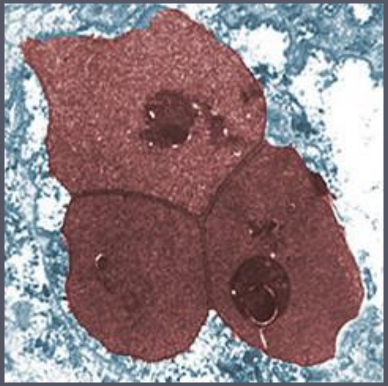
Parasite diversity and host immunity

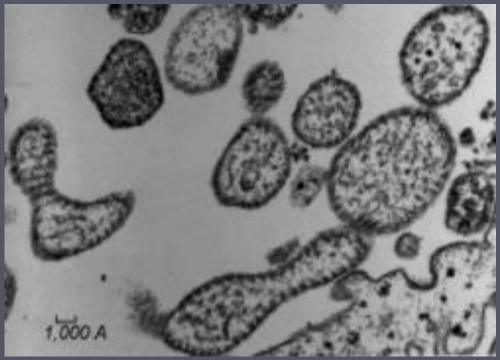
- Ex. an increase in the number of parasite species is associated with an increase in investment in the mammalian immune response (Nunn et al. 2000, 2002)



Parasite diversity and host mortality

- Higher diversity of parasites worsens the negative impact of parasitism to the host
- ex. coinfection of canine distemper virus (CDV) and heamoparasite (*Babesia* sp.) leads to high mortality of African lions in Tanzania





Babesia

Munson et al. 2008 , Plos One

Biogeographical aspects of parasite diversity

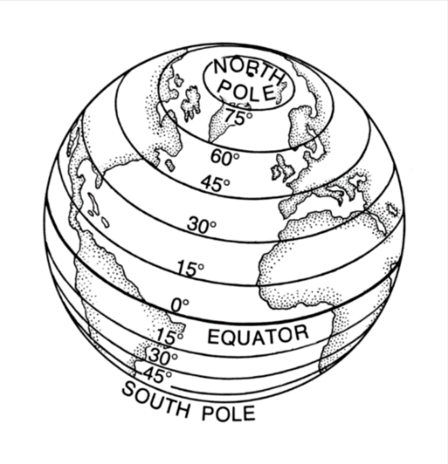
- Biogeographical rules - changes of species diversity applicable to parasites
- Latitude gradient
- Preferred centre model versus local oasis model
- Shift of similarity of parasite diversity with distance, i.e. the role of geographical distances to similarity of parasite communities

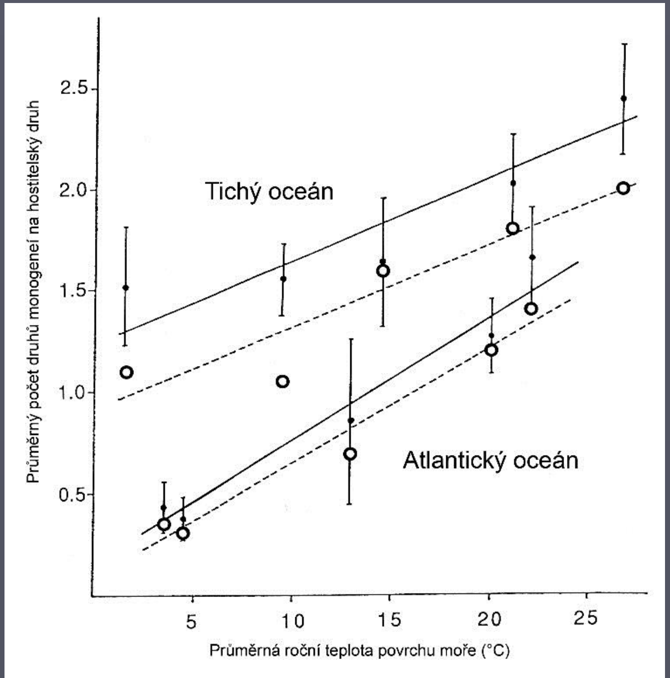
Latitudinal gradient

- Latitude - the main biogeographical factor influencing the diversity of parasites

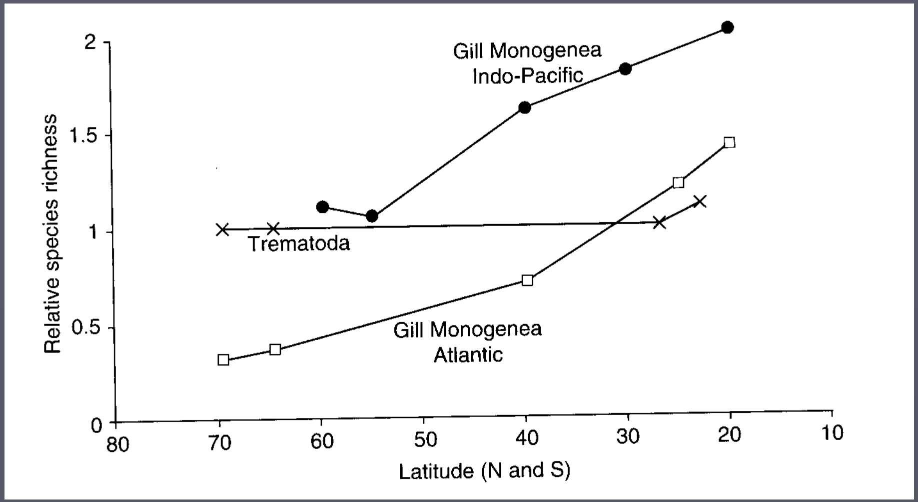
- High diversity in the tropics due to higher evolutionary speed

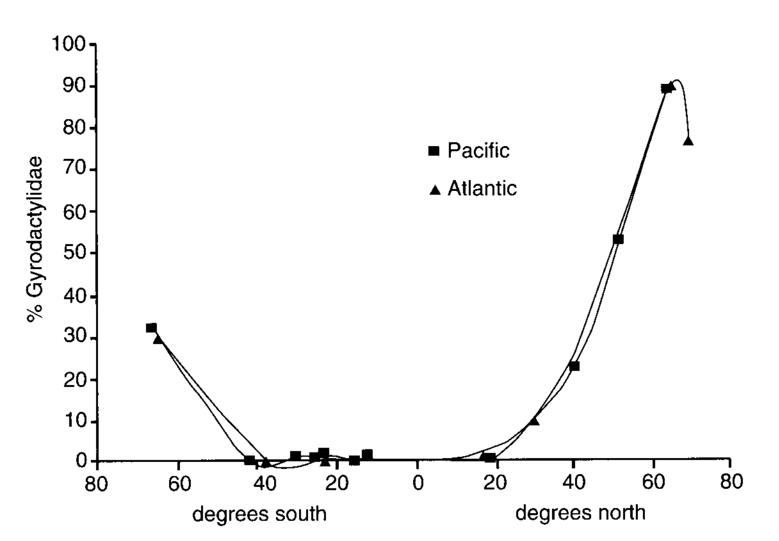
- Some climatic factors (temperature) show a similar trend in the relationship to the diversity of ectoparasites in particular





Latitudinal gradient





Ex. Species diversity of digeneans and monogeneans in marine fish depending on latitude

Ex. Representation of marine Gyrodactylidae (in relation to all gill Monogenea) on the gills of sea fish in relation to latitude

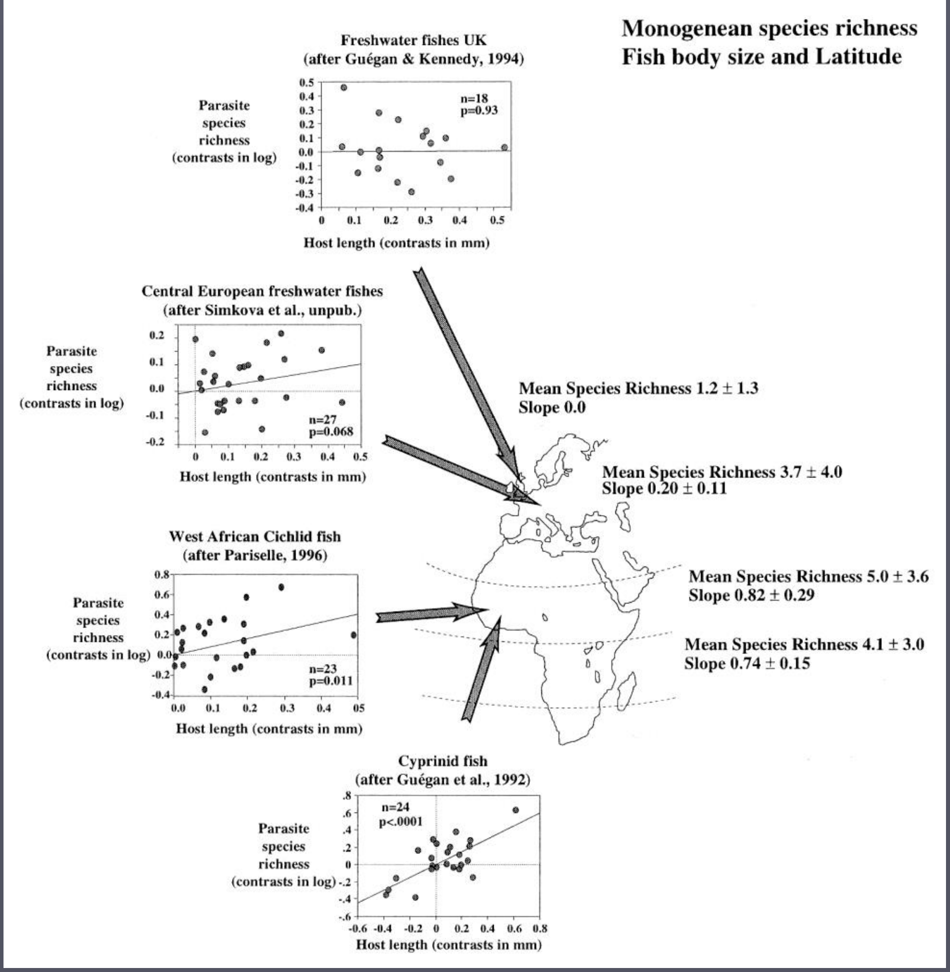
Latitudinal gradient

- Causes of latitudinal gradient - multiple mechanisms
- Area size theory: larger area - more species
- Species-area theory: larger tropics - higher diversity
- Species-energy theory: more energy, more biomass in a given area, higher diversity
- Theory of ecological time
- Climate stability theory

- Mid-domain model - different centre of species distribution - geographical or climatic centre or marginal centre

Latitudinal gradient

- It affects the relationship between host size and parasite diversity



Number of species on the island

$D = S^b$, $b = 0.2\text{-}0.3$

Number of monogenean species on the gills of fish

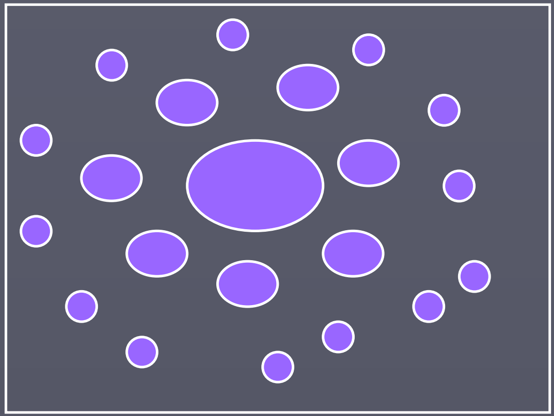
$A = aW^b$, $W = L^3$ and $b = 0.8$

$P = ((L^3)^{0.8})^{0.2}$ and $P = ((L^3)^{0.8})^{0.3}$

$\rightarrow P = L^{0.48}$ and $P = L^{0.72}$

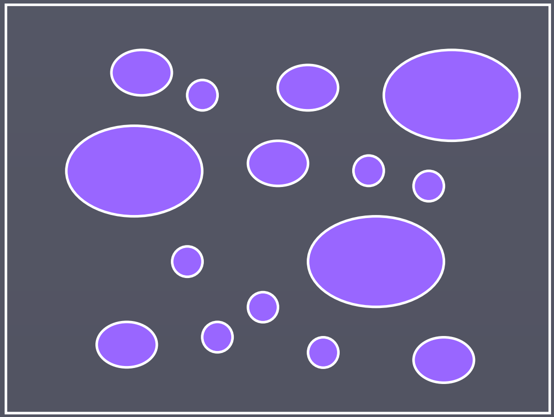
Preferred centre or local oasis?

- Preferred centre model (abundance centre model)
  - unimodal distribution of species abundance in space
  - geographical distances between each site and the reference site (i.e. the site with the highest abundance of the species)



- Model of local oases
  - multimodal distribution of abundance of the species in space

  Methodologically not yet determined



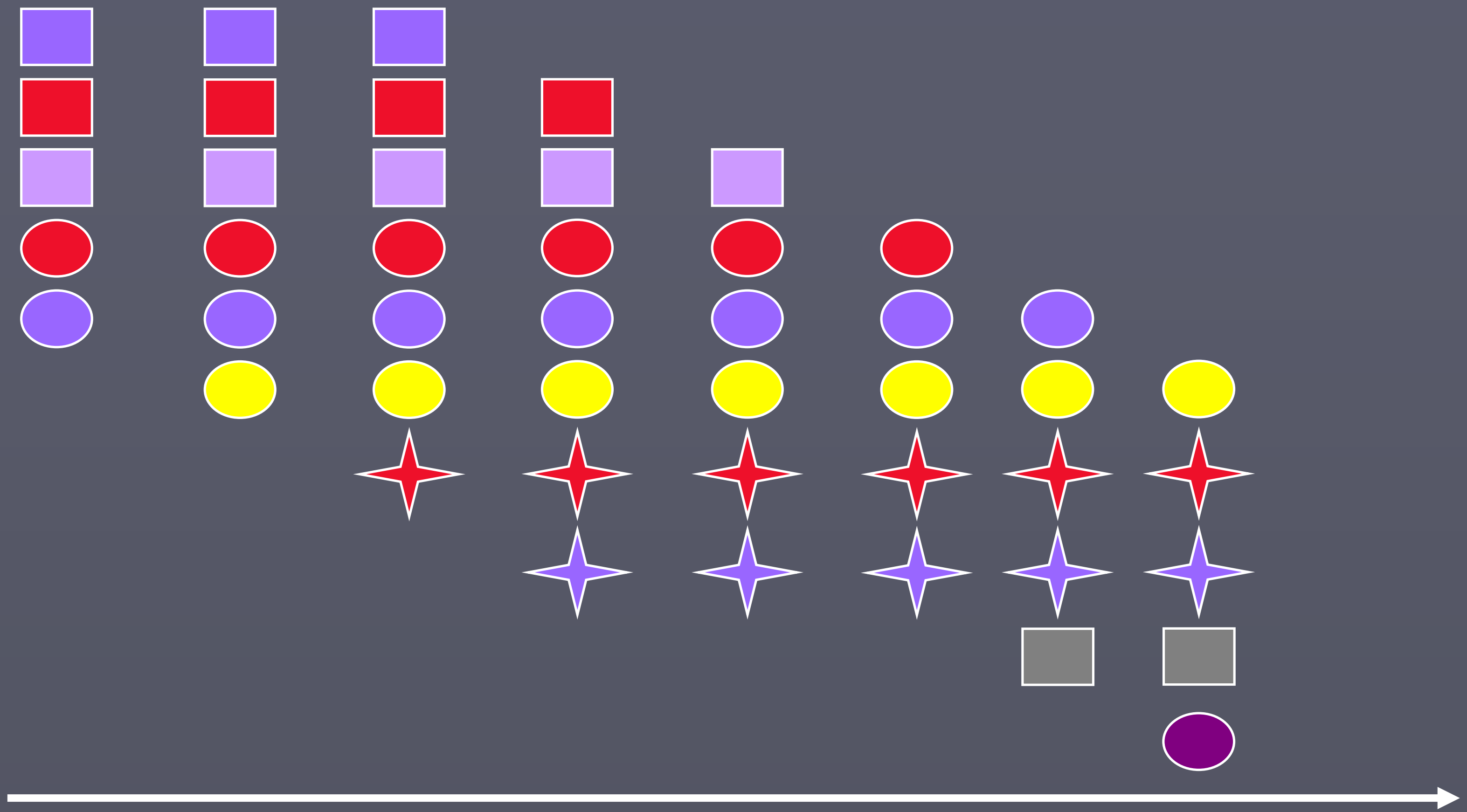
Preferred centre model

- Study of 8 species of helminths in fish species *Perca flavescens* (Poulin & Dick, 2007) - only the prevalence of *Proteocephlaus pearsei*

- Study of metazoan parasites in fish species *Squalius cephalus* (Seifertová et al., 2008) - Monogenea

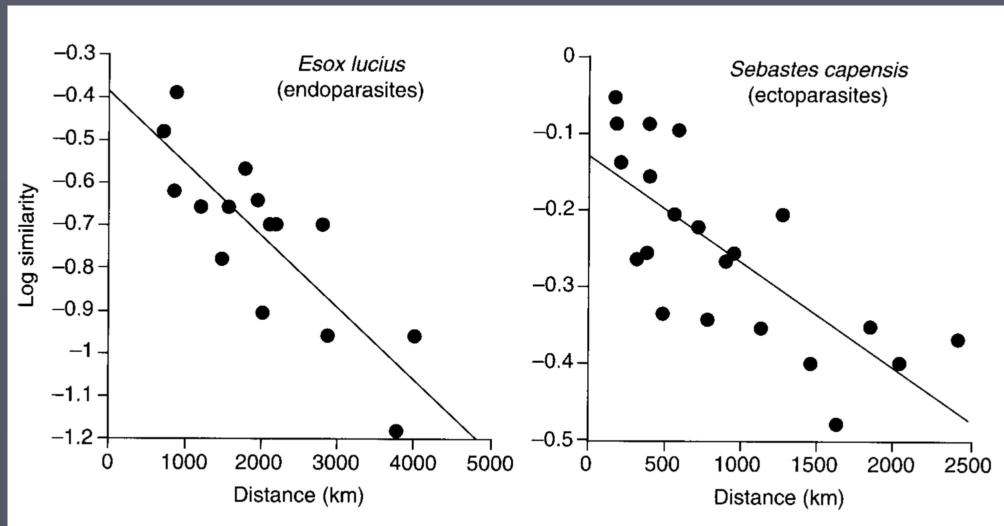
- Study of 22 species of fleas and mites in rodents (Krasnov et al., 2008) - weak relationship

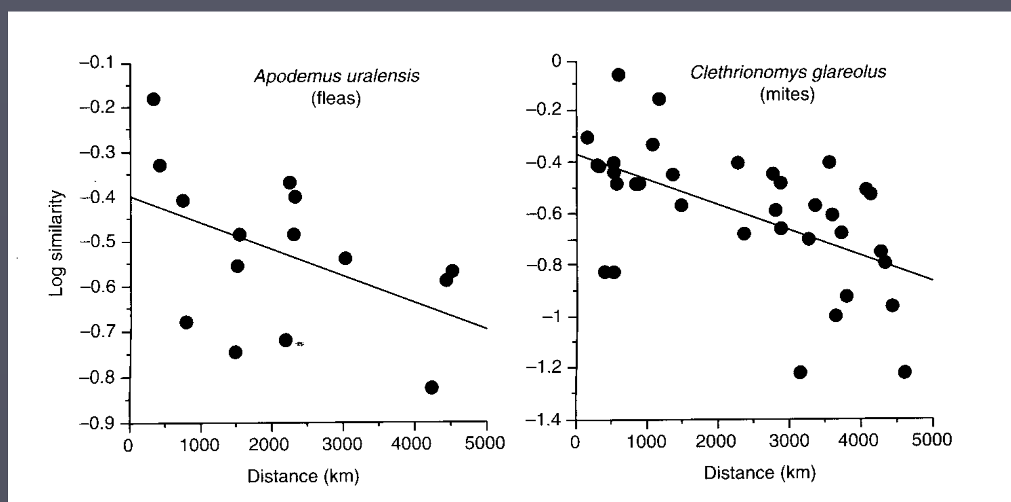
Shift of geographical distances



Geographical distances
Climatic or environmental gradient
Species-specific dispersion limits

Shift of geographical distances





Ex. Flea communities Ex. Mite communities

Shift in parasite diversity affected by host genetic distances

- similarity between communities of metazoan parasites in populations *Squalius cephalus* (Seifertová et al. 2008)