The Ecology of Emerging Tick-borne Diseases in a Changing World
Emerging infectious diseases, 1940-2004
(335 total)

Jones et al. Nature 2008
Emerging infectious diseases, 1940-2004
(335 total)

Zoonotic
75%
The EID dominant paradigm

1. Identify the pathogen
2. Identify the reservoir
3. Identify the vector
4. Kill one of them
5. Urge surveillance
Are there general principles that can guide us?

1. Zoonotic pathogens are “multi-host” pathogens
2. But only some hosts amplify the pathogen, others diminish or “dilute”
3. Changes in the **abundance or effect** of these amplifiers and diluters may help predict outbreaks
United States. Data from the CDC.

Lyme disease cases

Year

Lyme disease

Multiply by 10

Babesiosis, New York State (data from NYSDOH)

Human babesiosis cases

Year

Granulocytic anaplasmosis

Number of Anaplasmosis Cases

Year of Report
Pathogens acquired from vertebrate hosts
Nymphs transmit vast majority of infections

Ixodes scapularis ticks

abundance
infection prevalence
Which hosts infect ticks with these three pathogens (i.e. are pathogen “amplifiers”)?
1. Collect replete larvae from known host
2. Incubate until molted into nymphal stage
3. Extract DNA and conduct qPCR for 3 tick-borne pathogens
Reservoir competence for *Borrelia burgdorferi*

Keesing et al. 2009 *PRSB* and LoGiudice et al. 2003 *PNAS*
Reservoir competence for *Babesia microti*

Hersh, Keesing *et al.* (2012), Emerging Infectious Diseases
Reservoir competence for *A. phagocytophilum*

Keesing et al. 2012 *Emerging Infectious Diseases*
Which hosts permit tick survival while feeding (i.e. are tick “amplifiers”)?
Host “permissiveness”

Capture wild mice, chipmunks, veeries, squirrels, opossums, catbirds in August

Hold in lab until tick-free

Inoculate with 100 larval ticks

Dead ticks Live ticks
Host permissiveness

<table>
<thead>
<tr>
<th>Host species</th>
<th>Proportion of larval ticks fed (+SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mouse</td>
<td>0.5</td>
</tr>
<tr>
<td>Veery</td>
<td>0.3</td>
</tr>
<tr>
<td>Catbird</td>
<td>0.3</td>
</tr>
<tr>
<td>Chipmunk</td>
<td>0.3</td>
</tr>
<tr>
<td>Squirrel</td>
<td>0.2</td>
</tr>
<tr>
<td>Opossum</td>
<td>0.1</td>
</tr>
</tbody>
</table>

F = 19.54, P < 0.001

A PATTERN:
the same small mammals are the best reservoirs and hosts

two causes:
adaptation by hosts and pathogens

two consequences:
coinfection and biodiversity loss
FOUR CONSEQUENCES:
• Coinfection
• Biodiversity loss
• Food supply
• Predators
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188 sites sampled for *I. scapularis* nymphs throughout Dutchess County, 2010-2012
Questing nymphs

Graph showing mean percent ticks infected (per site) for Anaplasma (Ap), Babesia (Bm), and Borrelia (Bb).

Map of study area with black dots representing sample locations.

Hersh et al. PLOS ONE 2014
Questing nymphs
4368 Questing nymphs

Hersh et al. PLOS ONE 2014
ONE CONSEQUENCE: coinfection

3275 ticks from 181 known hosts

Hersh et al. PLOS ONE 2014
THE SECOND CONSEQUENCE:
increased risk with biodiversity loss

Fast life history & abundant → Resilient to disturbance/biodiversity loss → Dominant in low-diversity communities
Community disassembly and nestedness

Which species remain when biodiversity is lost?
Species

Most ubiquitous species

Most diverse fragment

Significantly nested, $P < 0.001$
Species

Fragments

w-f mouse
s-t shrew
chipmunk
Allan et al. Con Bio 2003

\[ R^2 = 0.646, P < 0.01 \]

Density of Infected Nymphs (Infected Nymphs/m²) vs. Area (ha)

\[ \text{Density of Infected Nymphs} \]
High biodiversity reduces Lyme risk

More diverse animal communities have more host species that:
• Hoover up ticks and kill them, and
• Fail to infect those ticks that survive
Generality?
IF: Hosts differ in quality (competence) for pathogens (and vectors)

AND: The most competent host(s) remain when biodiversity declines

THEN: Disease transmission increases with biodiversity loss

= “Dilution Effect”
Biodiversity inhibits parasites: Broad evidence for the dilution effect

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Infectious diseases of humans, wildlife, and domesticated species are increasing worldwide, driving the need to understand the mechanisms that shape outbreaks. Simultaneously, human activities are drastically reducing biodiversity. These concurrent patterns have prompted repeated suggestions that biodiversity and disease are linked. For example, the dilution effect hypothesis posits that these patterns are causally related; diverse host communities inhibit the spread of parasites via several mechanisms, such as by regulating populations of susceptible hosts or interfering with parasite transmission. However, the generality of the dilution effect hypothesis remains controversial, especially for zoonotic diseases of humans. Here we provide broad evidence that host diversity inhibits parasite abundance using a meta-analysis of 202 effect sizes on 61 parasite species. The magnitude of these effects was independent of host density, study design, and type and specialization of parasites, indicating that dilution was robust across all ecological contexts examined. However, the magnitude of dilution was more closely related to the frequency, rather than density, of focal host species. Importantly, observational studies overwhelmingly documented dilution effects, and there was also significant evidence for dilution effects of zoonotic parasites of humans. Thus, dilution effects occur commonly in nature, and they may modulate human disease risk. A second analysis identified similar effects of diversity in plant–herbivore systems. Thus, although there can be exceptions, our results indicate that biodiversity generally decreases parasitism and herbivory. Consequently, anthropogenic declines in biodiversity could increase human and wildlife diseases and decrease crop and forest production.

There is support for dilution effects and the key underlying mechanisms in some systems (8, 14–16). Despite this, the generality of the dilution effect hypothesis remains contentious debated (13, 17, 18). For example, parasite dynamics may be driven by the identity of the particular species present, rather than disease per se (17). In addition, some undisturbed habitats (e.g., intact forests) can contain higher densities of parasites or vectors than disturbed sites (13, 18). However, such comparisons can inappropriately equate habitat disturbance with biodiversity loss while ignoring other confounding factors (19).

We addressed the generality of the dilution effect hypothesis with a formal meta-analysis. We searched the published literature for all available data sources, including experimental and observational studies of human and wildlife diseases, to rigorously assess the generality of this phenomenon. We estimated the effect of biodiversity on parasite abundance using the Hedges’ g effect size (thus negative values indicate dilution effects) and used a multilevel model to include nonindependence among effect sizes that arise from the same parasite species or experiments. Last, we compared the evidence for dilution effects with the evidence for associational resistance, an analogous hypothesis that posits that plant diversity inhibits the abundance of herbivores via mechanisms similar to those hypothesized to drive dilution effects (20). If both of these natural enemies are

Significance

This research identifies the broad generality of dilution effects to a wide range of parasites and hosts. It also demonstrates that diversity may decrease diseases, and it suggests that future conservation policies may need to consider the role of biodiversity in disease regulation.
Meta-analysis on 202 effect sizes, 61 parasite species
D. Civitello, J. Rohr, and colleagues (PNAS 2015)
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FOUR CONSEQUENCES:
• Coinfection
• Biodiversity loss
• Food supply
• Predators
Regulation of disease risk by predator communities?

Ye olde catfood can method
126 sites in two consecutive years

Predator assemblages and tick infection
Eat rodents

Deflect tick meals from rodents

Eat few rodents
Displace other mesopredators

All common mesopredators (20 sites)
Important small mammal predator (55 sites)
All common mesopredators or bobcat (31 sites)
Or
Fox (45 sites)
Bobcat (12 sites)
Coyote (77 sites)
Coyote but no fox (55 sites)
Coyote but no small mammal predators (48 sites)
HYPOTHESIS:
Diverse predator assemblages will reduce tick-feeding on small rodents and therefore reduce disease risk
Binomial model, site as random effect, corrected for spatial autocorrelation

High functional diversity reduces the probability that ticks are infected.

Are there general principles that can guide us?

1. Host species vary in quality for multi-host pathogens and vectors
2. Amplifying hosts often occupy basal positions in communities
3. Impact of these amplifiers can increase when biodiversity is lost, resources surge, and predators decline or disappear
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