XXI WORKSHOP OF THE NATIONAL REFERENCE LABORATORIES FOR PARASITES
ISTITUTO SUPERIORE DI SANITÀ · ROME · 29 OCTOBER 2026

THE ECOLOGICAL DRIVERS BEHIND THE DYNAMICS OF THE EXPANSION OF ECHINOCOCCUS MULTILOCULARIS IN EUROPE

Alessandro Massolo

Ethology Unit, Department of Biology, University of Pisa, Pisa, Italy
Faculty of Veterinary Medicine, University of Calgary, AB, Canada



Why is E. multilocularis expanding in Europe…

…and why not everywhere?

Why is E. multilocularis expanding in Europe…
…and why not everywhere?

PATTERN

what the maps show

Why is *E. multilocularis* expanding in Europe…
…and why not everywhere?

PATTERN > **SCALE**

what the maps show

where processes act

Why is E. multilocularis expanding in Europe…
…and why not everywhere?

PATTERN › **SCALE** › **PROCESS**

what the maps show | where processes act | what the hosts do

Why is E. multilocularis expanding in Europe…
…and why not everywhere?

PATTERN › **SCALE** › **PROCESS** › **SURVEILLANCE**

what the maps show | where processes act | what the hosts do | what NRLs can do

A PARASITE THAT TRAVELS THROUGH A FOOD WEB

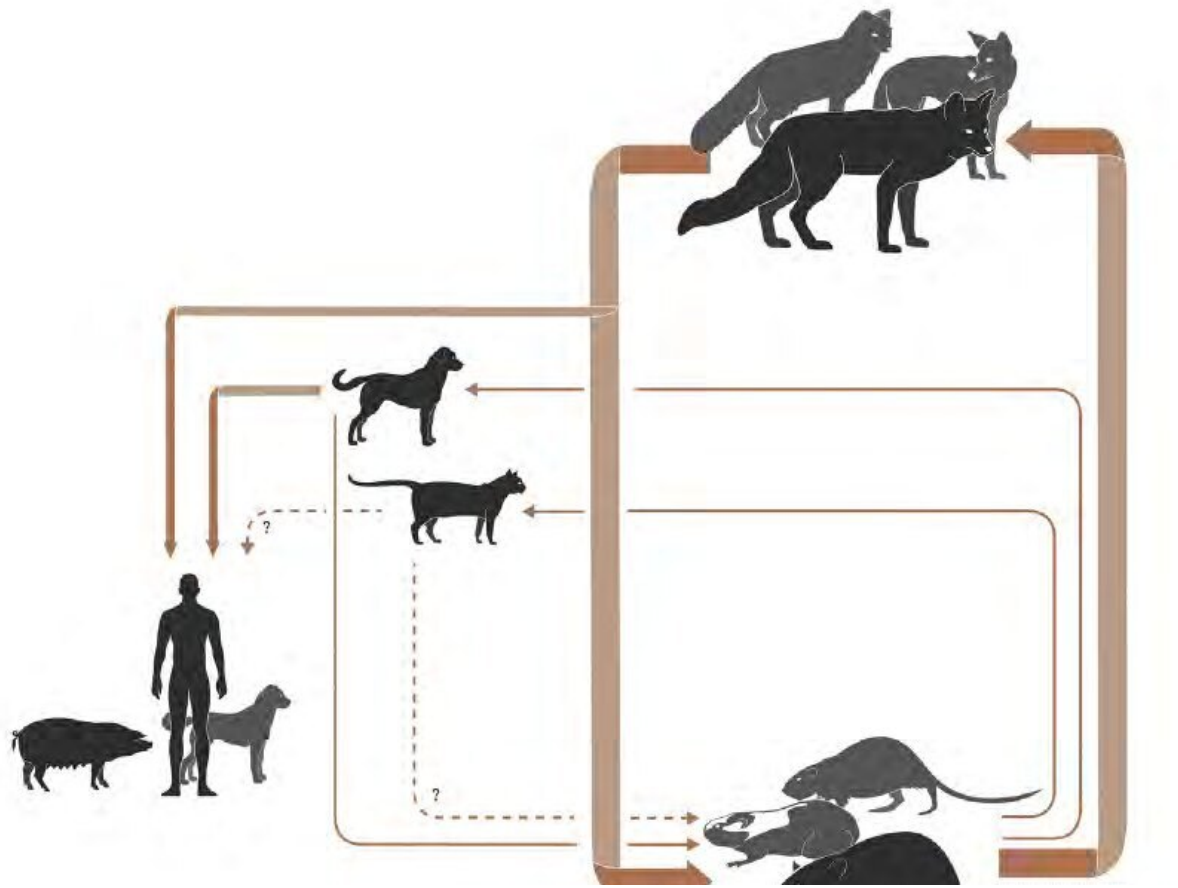
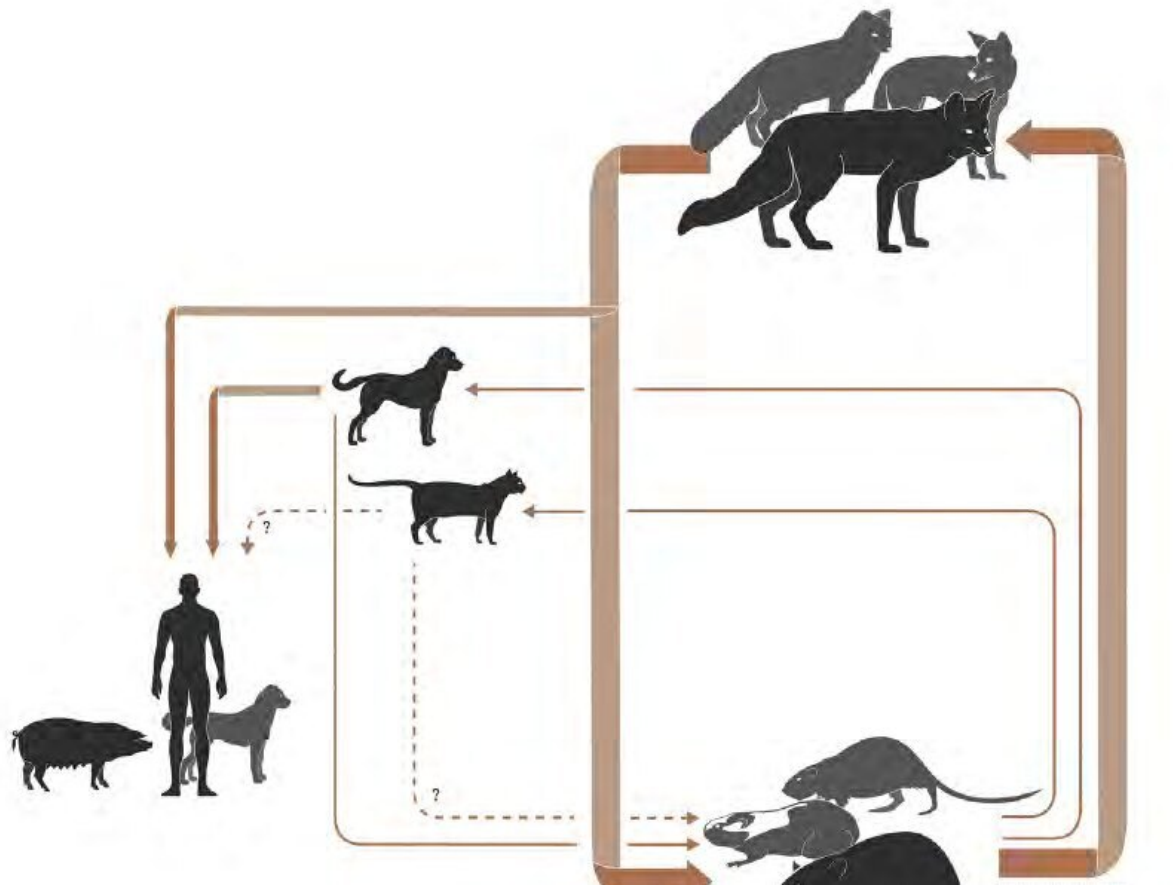
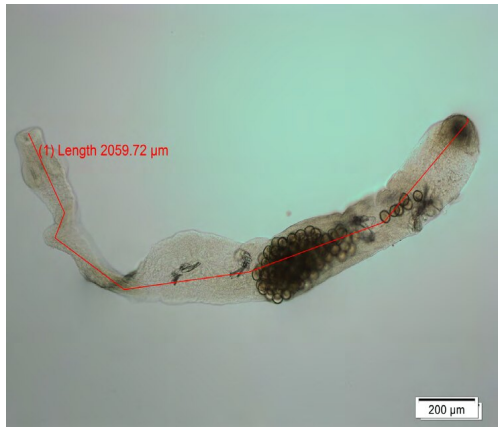


Figure: Romig et al. 2017, Adv Parasitol 95 · Mortality: Torgerson et al., in Cafiero et al. 2025, IJP-PAW

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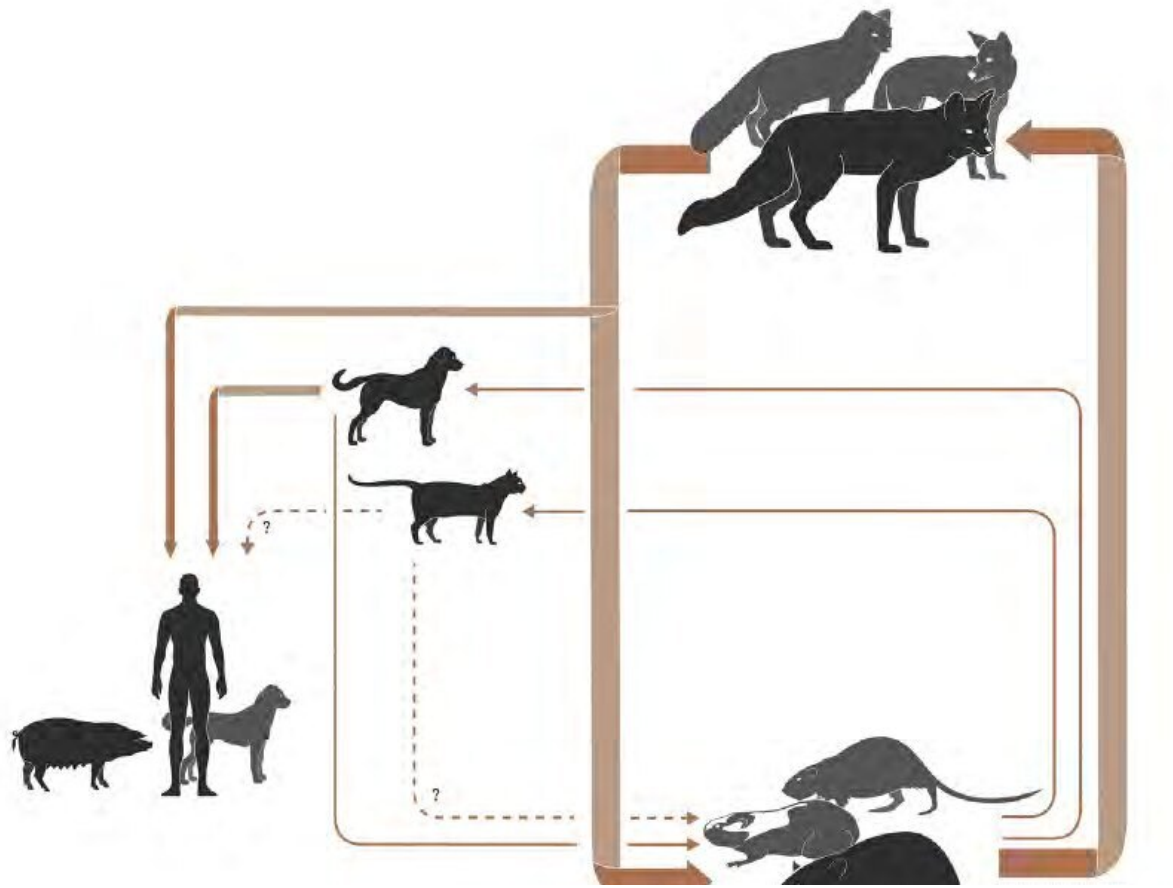


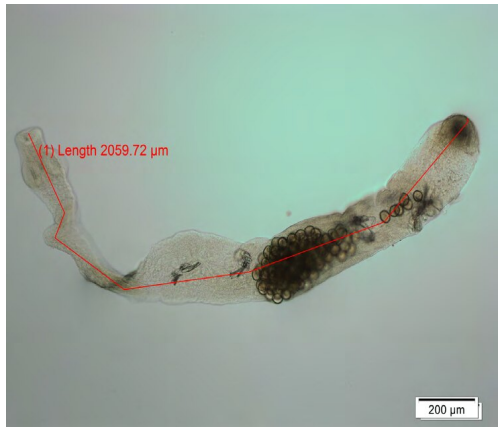
Adult worm: a few millimetres

Figure: Romig et al. 2017, Adv Parasitol 95 · Mortality: Torgerson et al., in Cafiero et al. 2025, IJP-PAW

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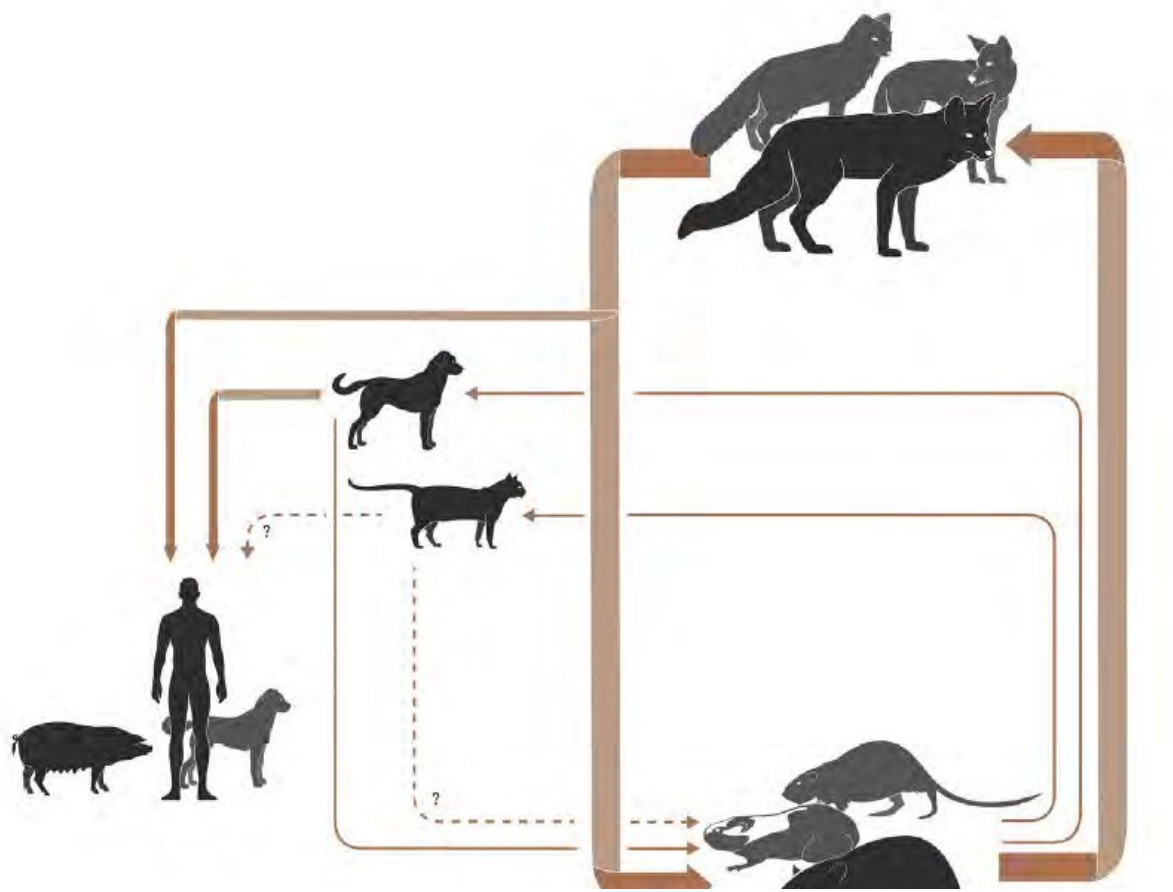
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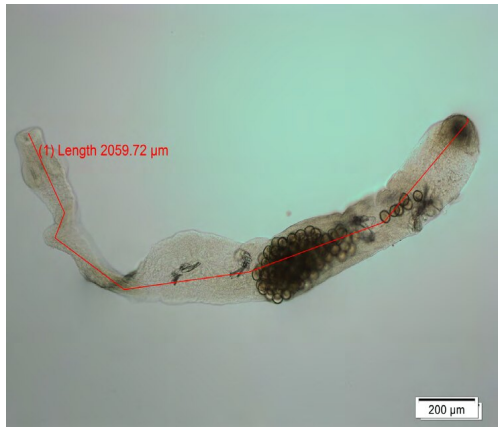
TRANSMISSION = WHO EATS WHOM, WHERE AND WHEN

Figure: Romig et al. 2017, Adv Parasitol 95 · Mortality: Torgerson et al., in Cafiero et al. 2025, IJP-PAW

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A PARASITE THAT TRAVELS THROUGH A FOOD WEB





Adult worm: a few millimetres

TRANSMISSION = WHO EATS WHOM, WHERE AND WHEN

Humans: accidental dead-end hosts – untreated AE is fatal in >90% of cases within 10–15 years

Figure: Romig et al. 2017, Adv Parasitol 95 · Mortality: Torgerson et al., in Cafiero et al. 2025, IJP-PAW

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THE PATTERN

What surveillance has shown – up to the 2015–2025 update

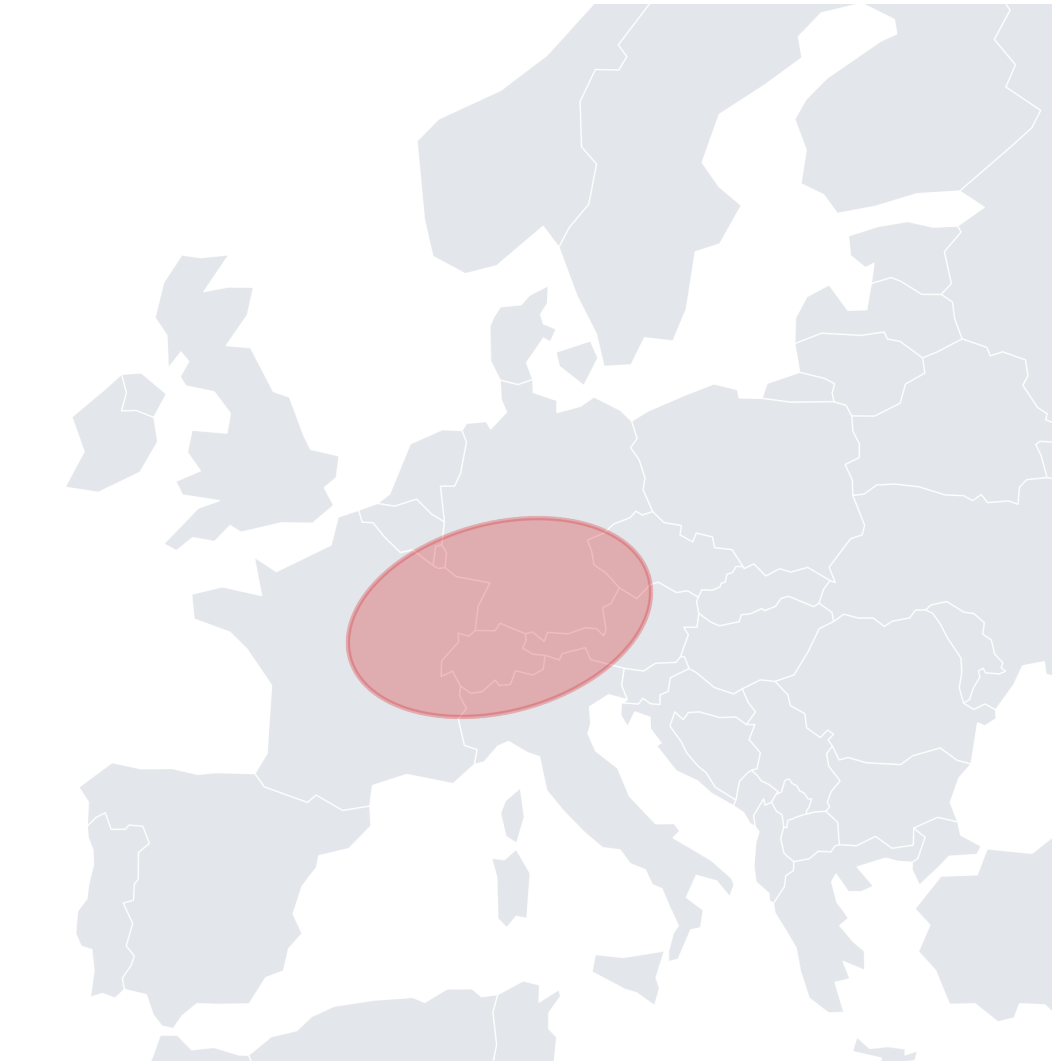


UNTIL THE 1990s: A CENTRAL-EUROPEAN PARASITE

Eckert et al. 2001; Oksanen et al. 2016, Parasit Vectors; WSAVA Congress Proceedings 2017

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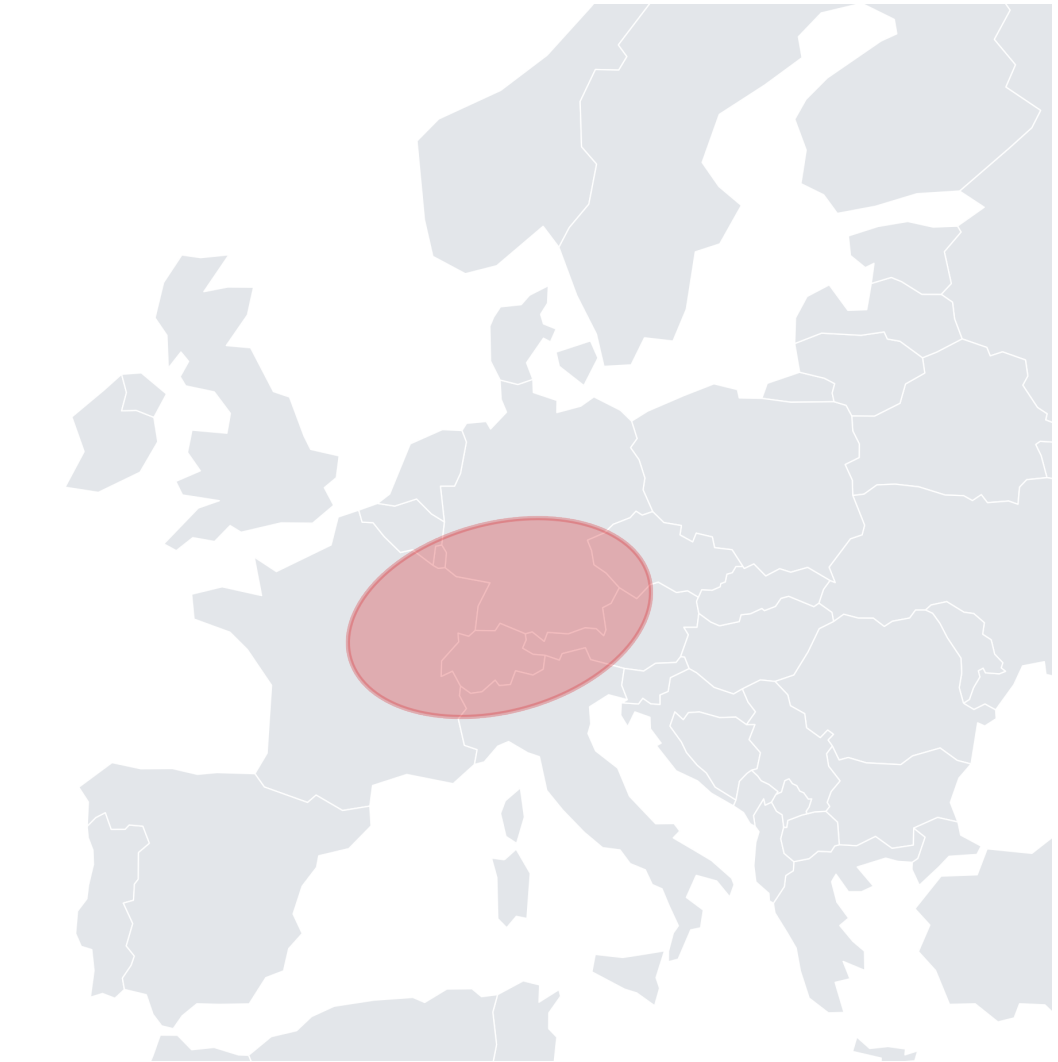


Historical core: eastern France, southern Germany, Switzerland, Austria

Eckert et al. 2001; Oksanen et al. 2016, Parasit Vectors; WSAVA Congress Proceedings 2017

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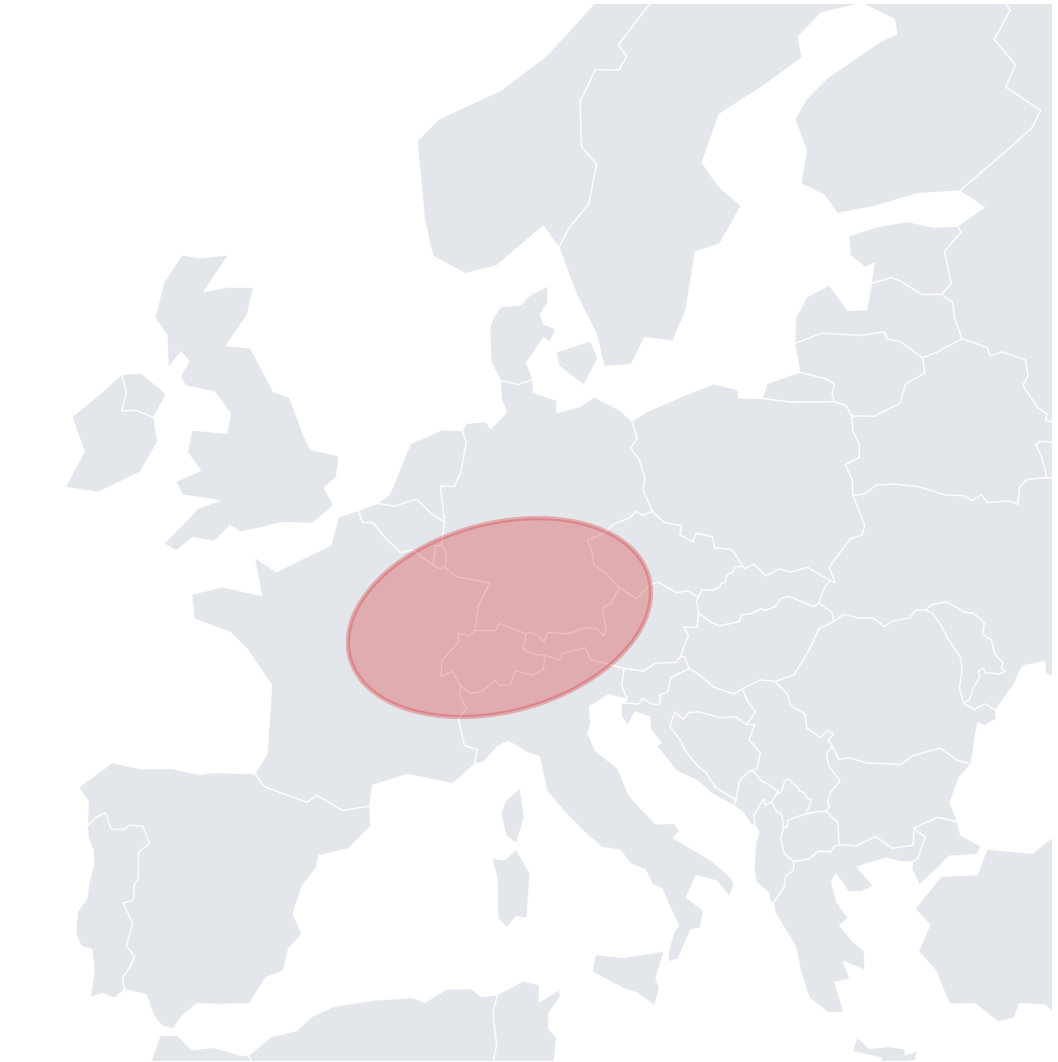
17

previously non-endemic European countries reported the parasite within three decades

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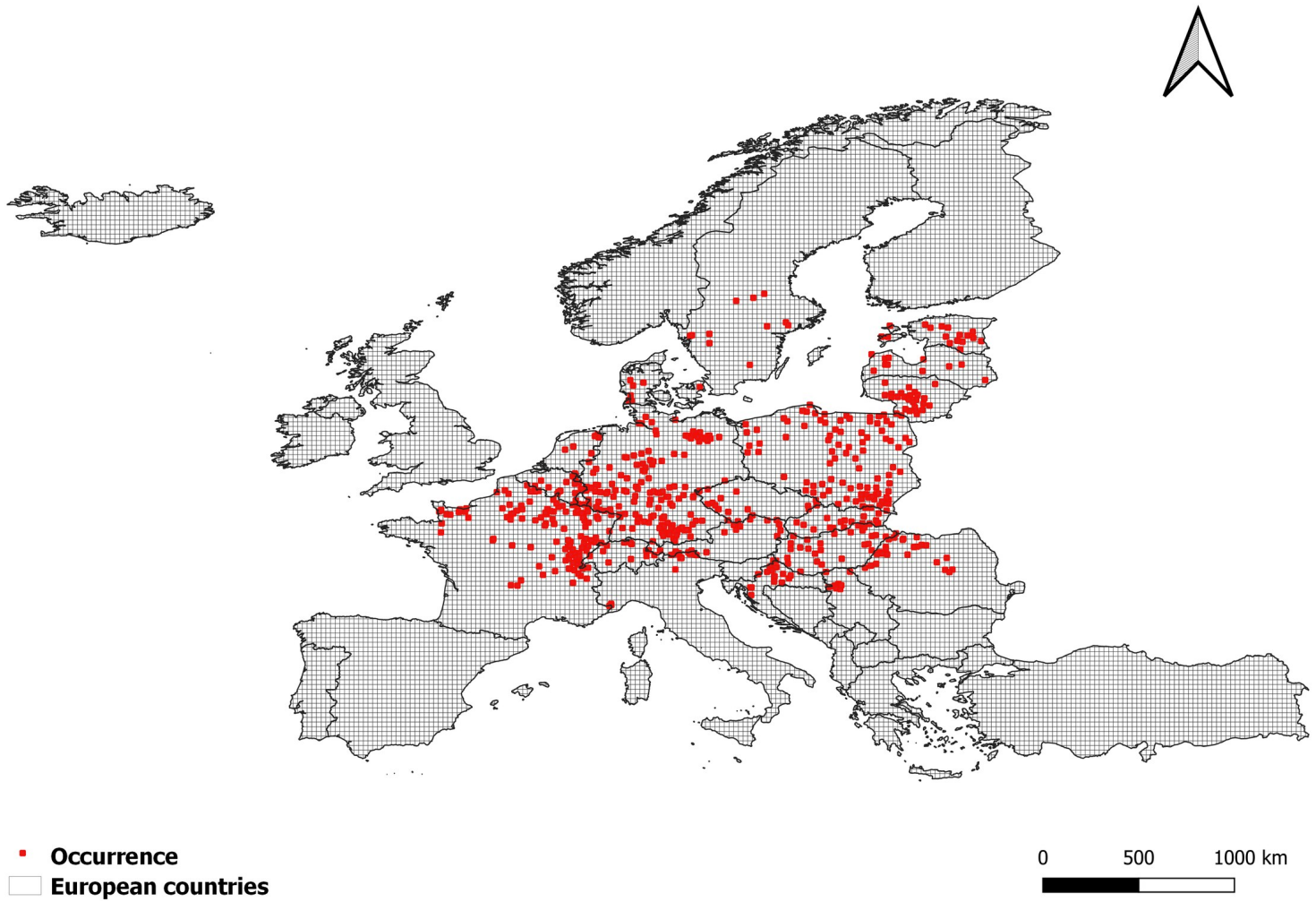
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EXPANSION… OR DISCOVERY?

Eckert et al. 2001; Oksanen et al. 2016, Parasit Vectors; WSAVA Congress Proceedings 2017

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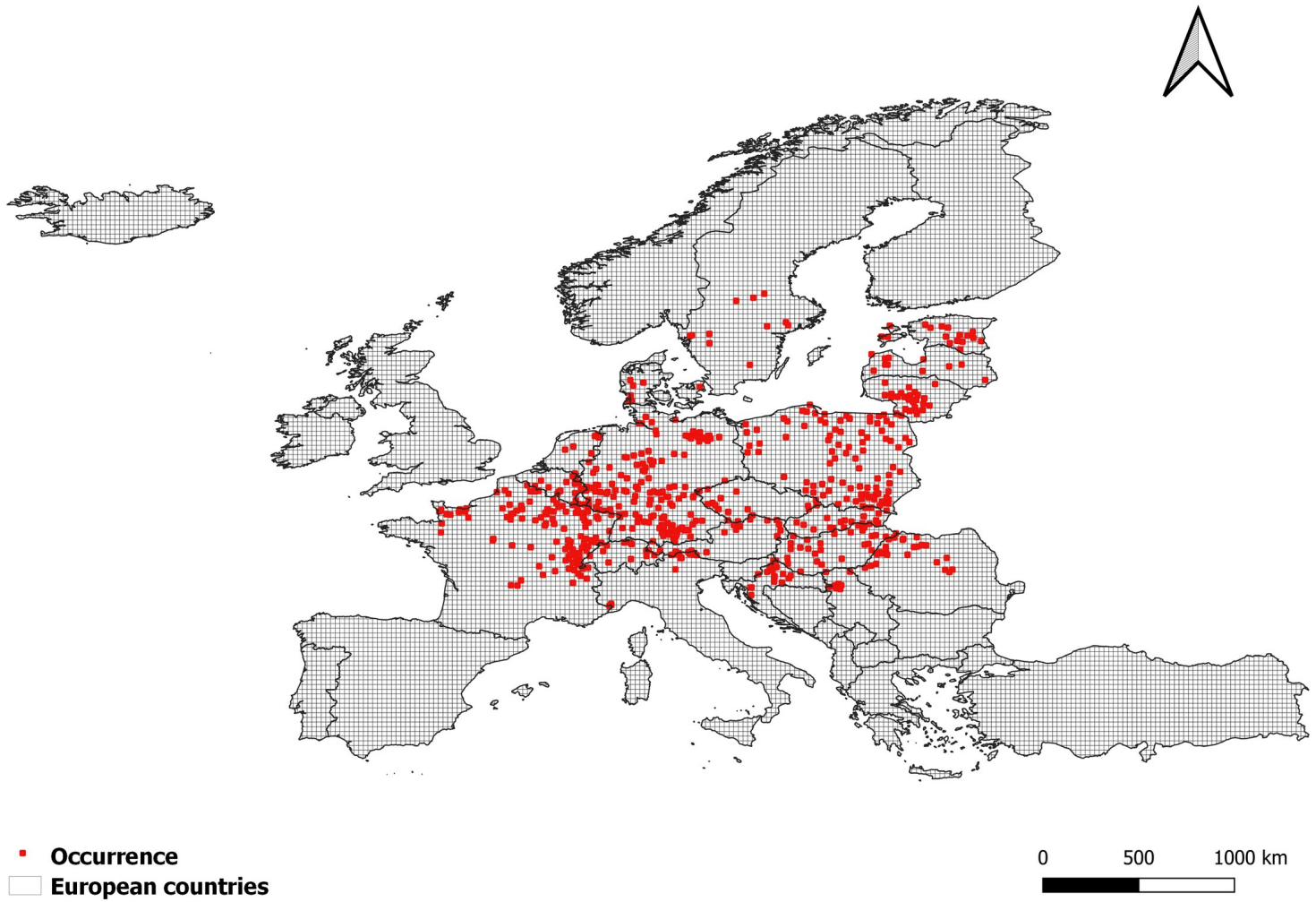
449 RELIABLE RECORDS, 35 YEARS OF LITERATURE



Oksanen et al. 2016, Parasit Vectors 9:519 · Cenni et al. 2023, Glob Change Biol 29:2436 · Umhang et al. 2014, Infect Genet Evol

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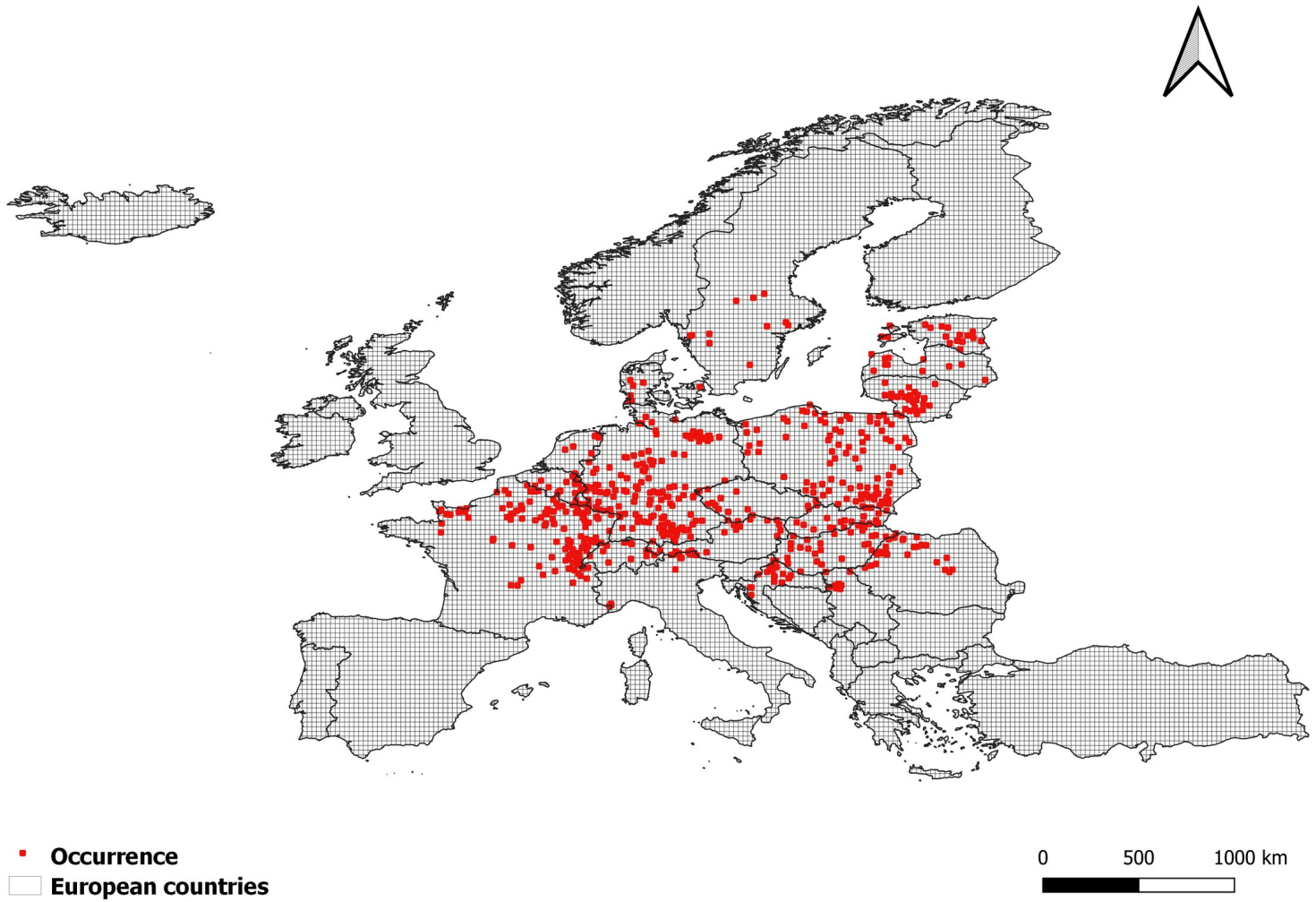
OKSANEN ET AL. 2016 · 1968–2014

Systematic review & meta-analysis for EFSA: the baseline of where *Em* was known

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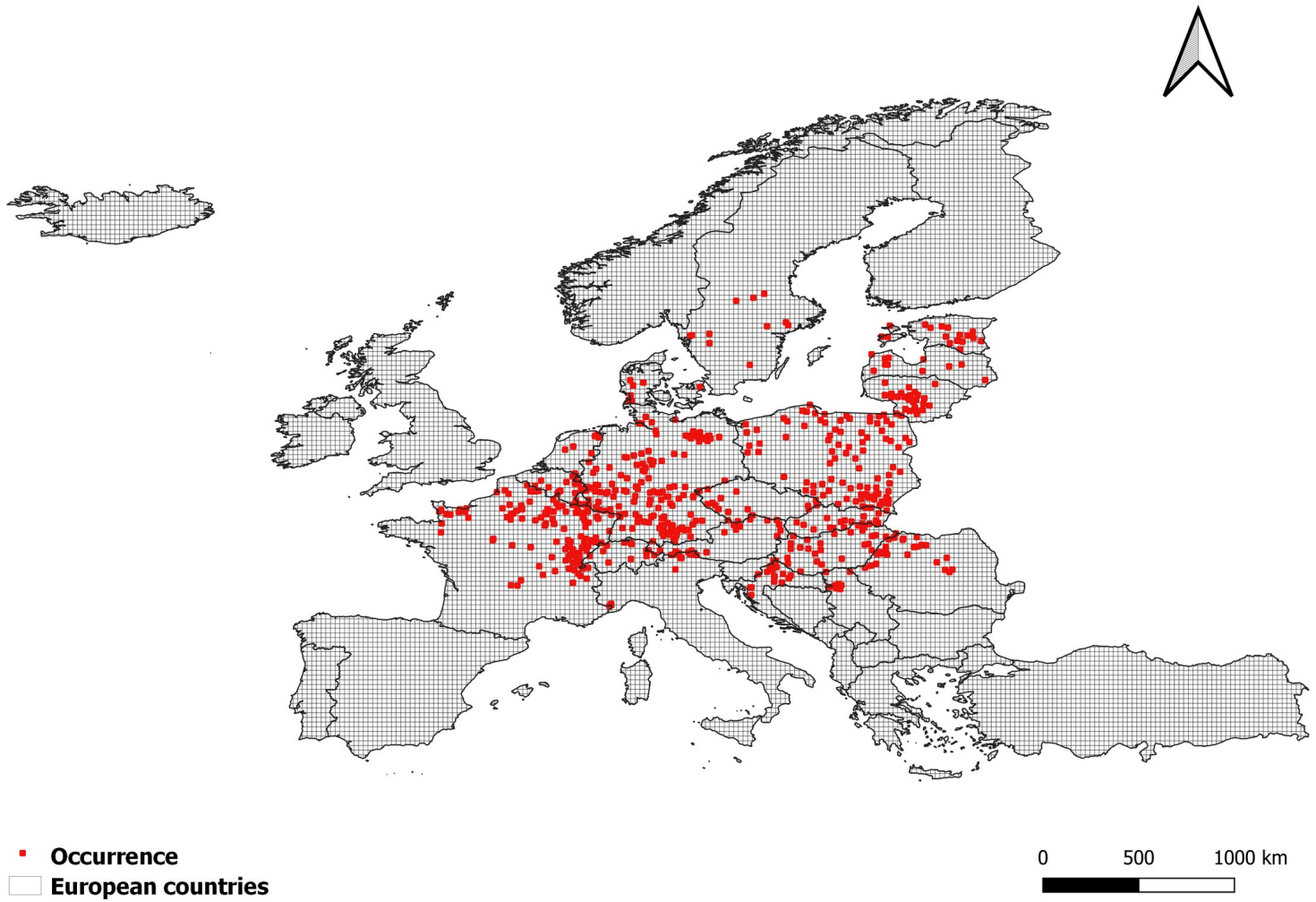
CENNI, SIMONCINI ET AL. 2023

449 georeferenced records used to model the niche **(presence only data)** at 25 × 25 km

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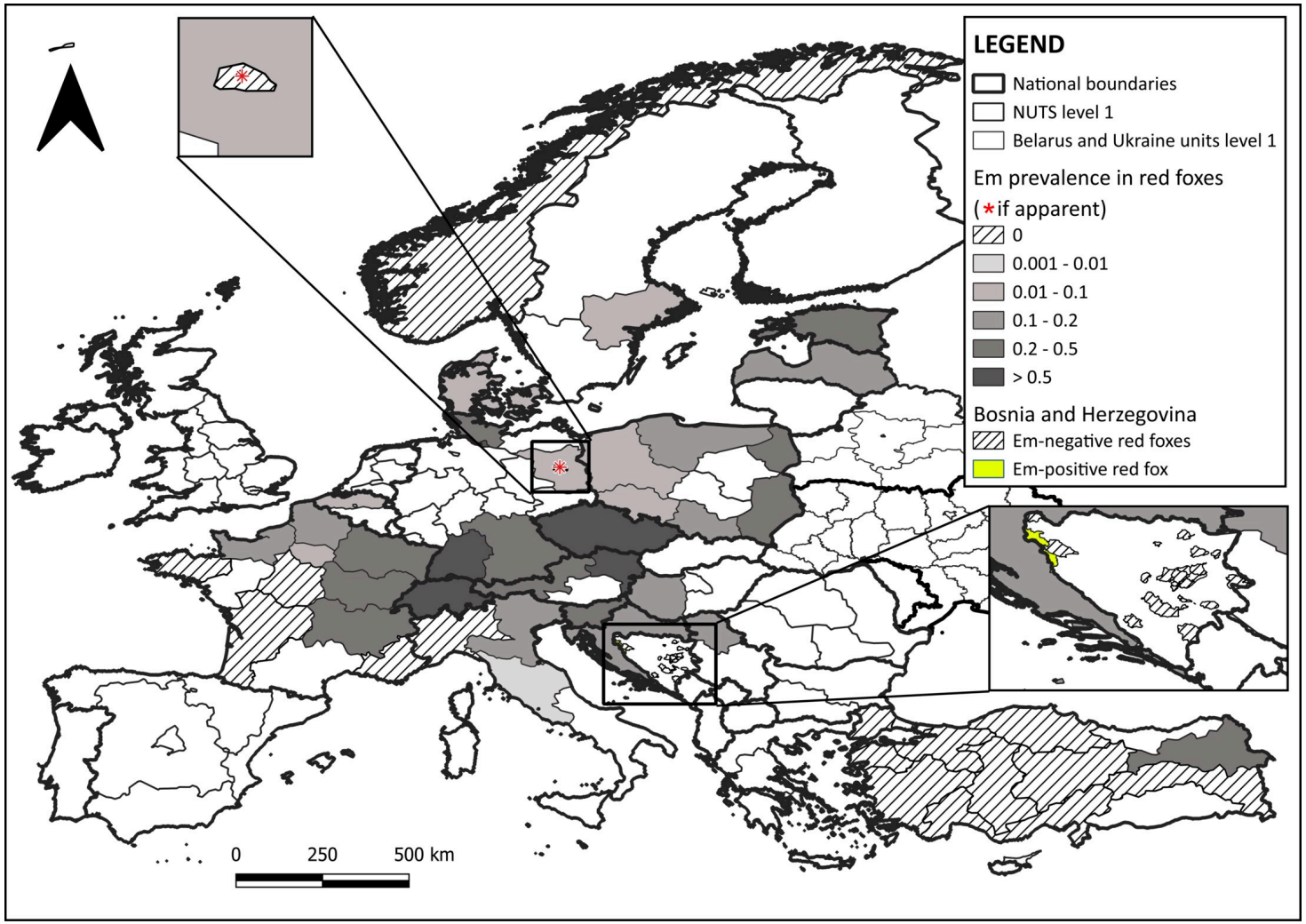
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EVERY MAP IS ALSO A MAP OF SAMPLING EFFORT

Oksanen et al. 2016, Parasit Vectors 9:519 · Cenni et al. 2023, Glob Change Biol 29:2436 · Umhang et al. 2014, Infect Genet Evol

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2015–2025: NOT A WAVE, A MOSAIC

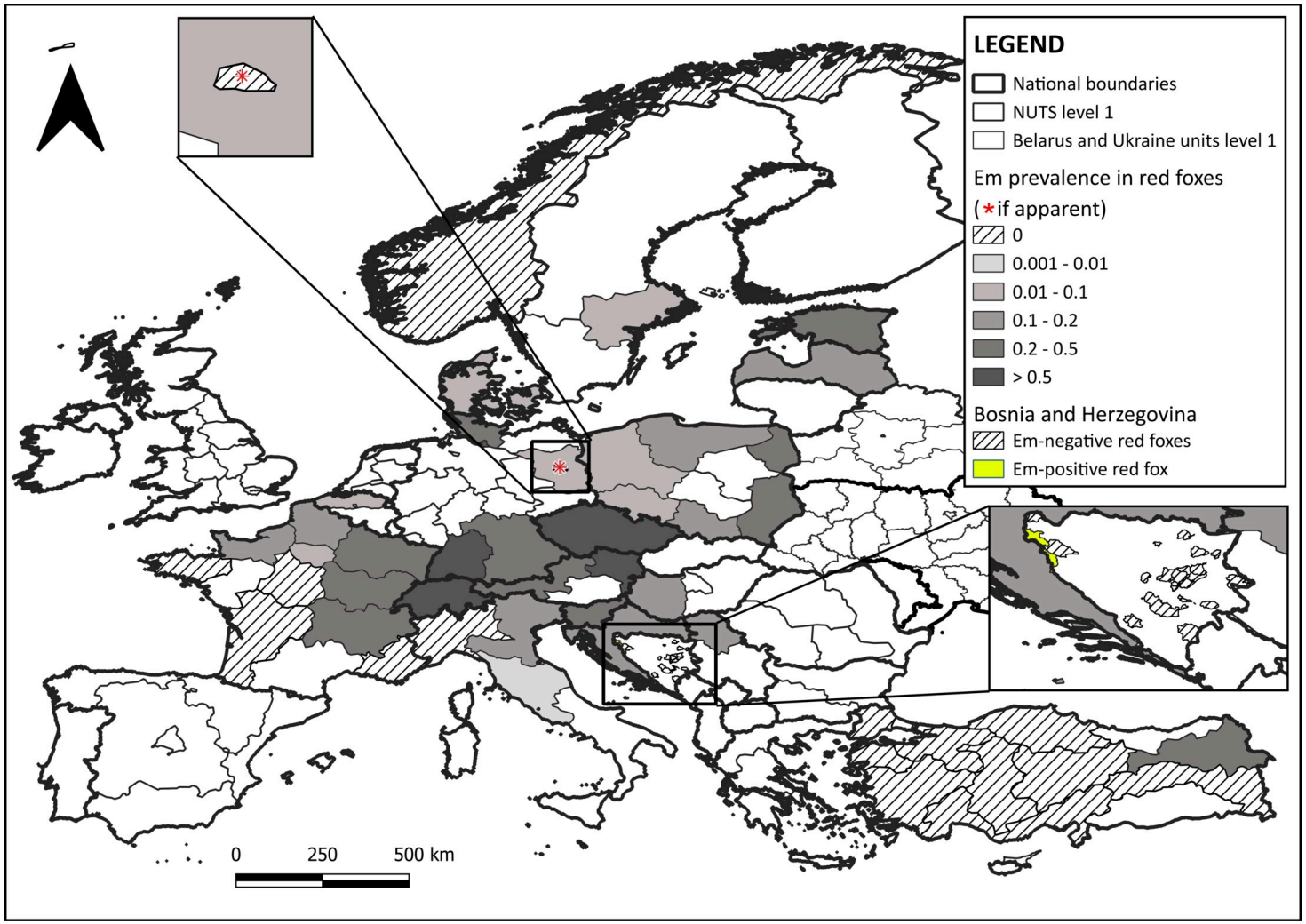


RED-FOX TRUE PREVALENCE · 88 PAPERS

Cafiero, Colla, Casulli & Massolo 2026, Parasit Vectors – SR & meta-analysis 2015–2025 (Figs 2–3)

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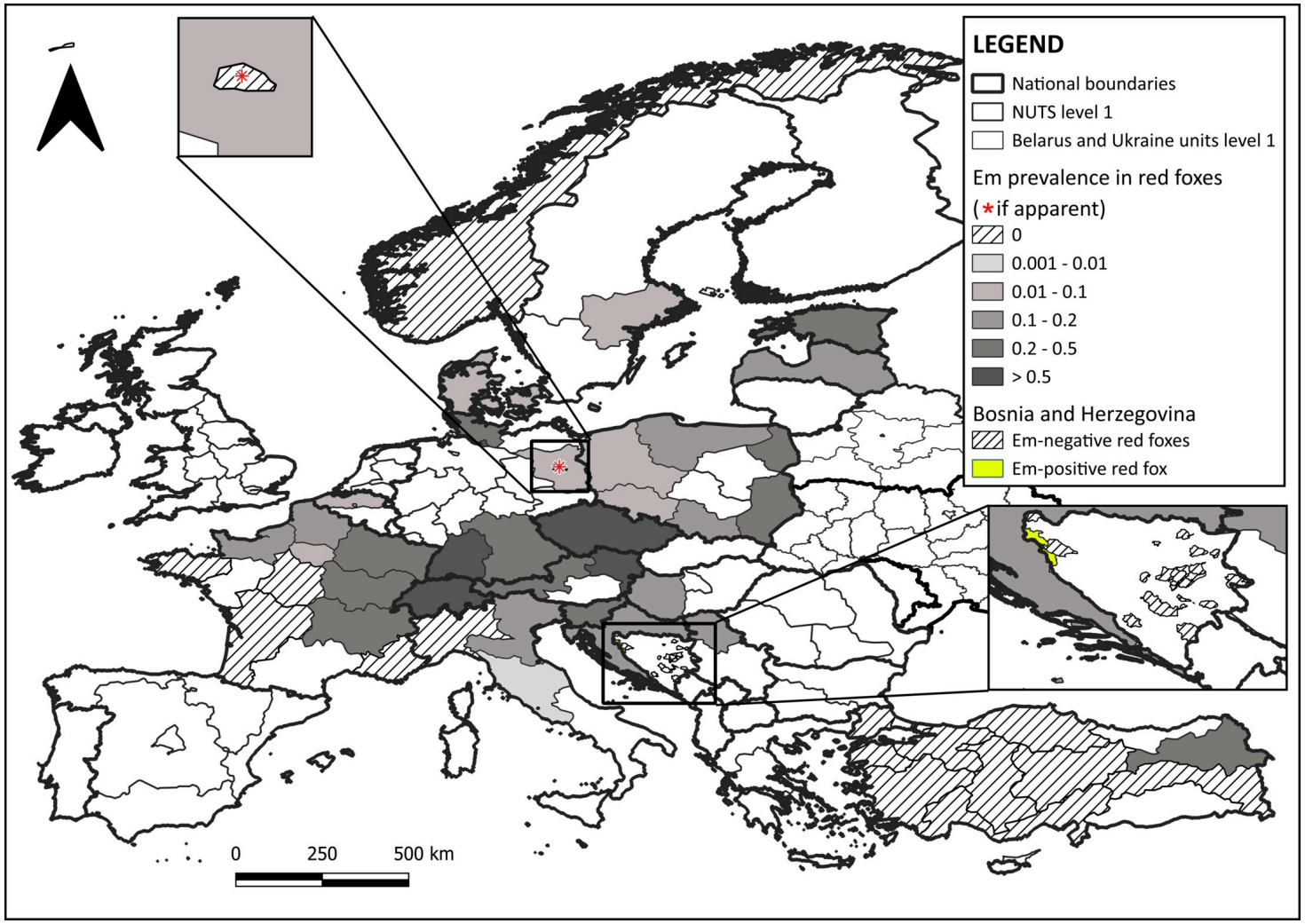
▲ RISING

E Austria · Denmark · SE France · SW Germany · SW Hungary · NE Italy · NW & SE Poland · Slovenia · E-Middle Sweden · Switzerland

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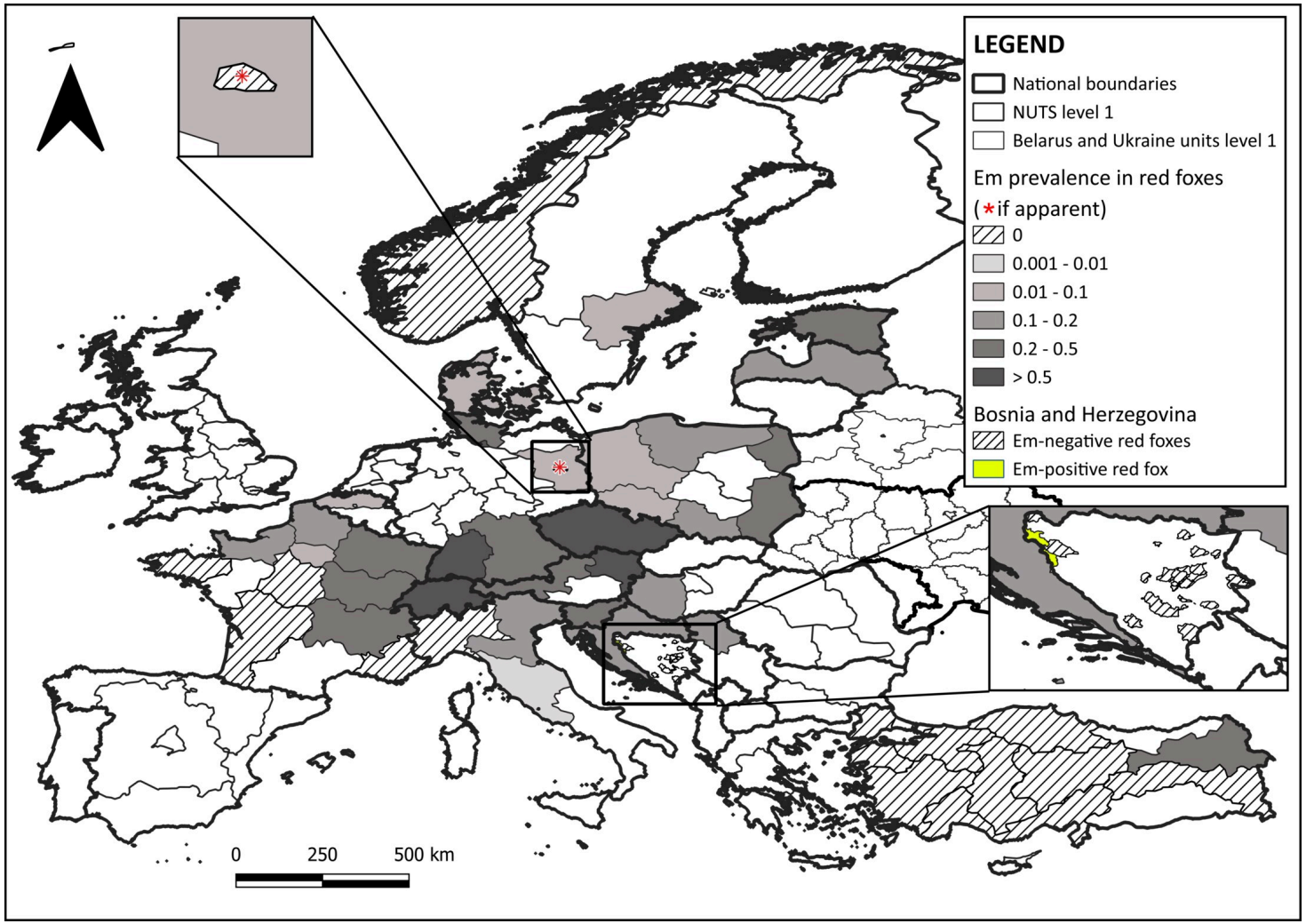
▼ DECLINING

Latvia · NE & E-central France · NE Poland; raccoon dogs NE Germany; water voles N Switzerland; Arctic foxes Svalbard

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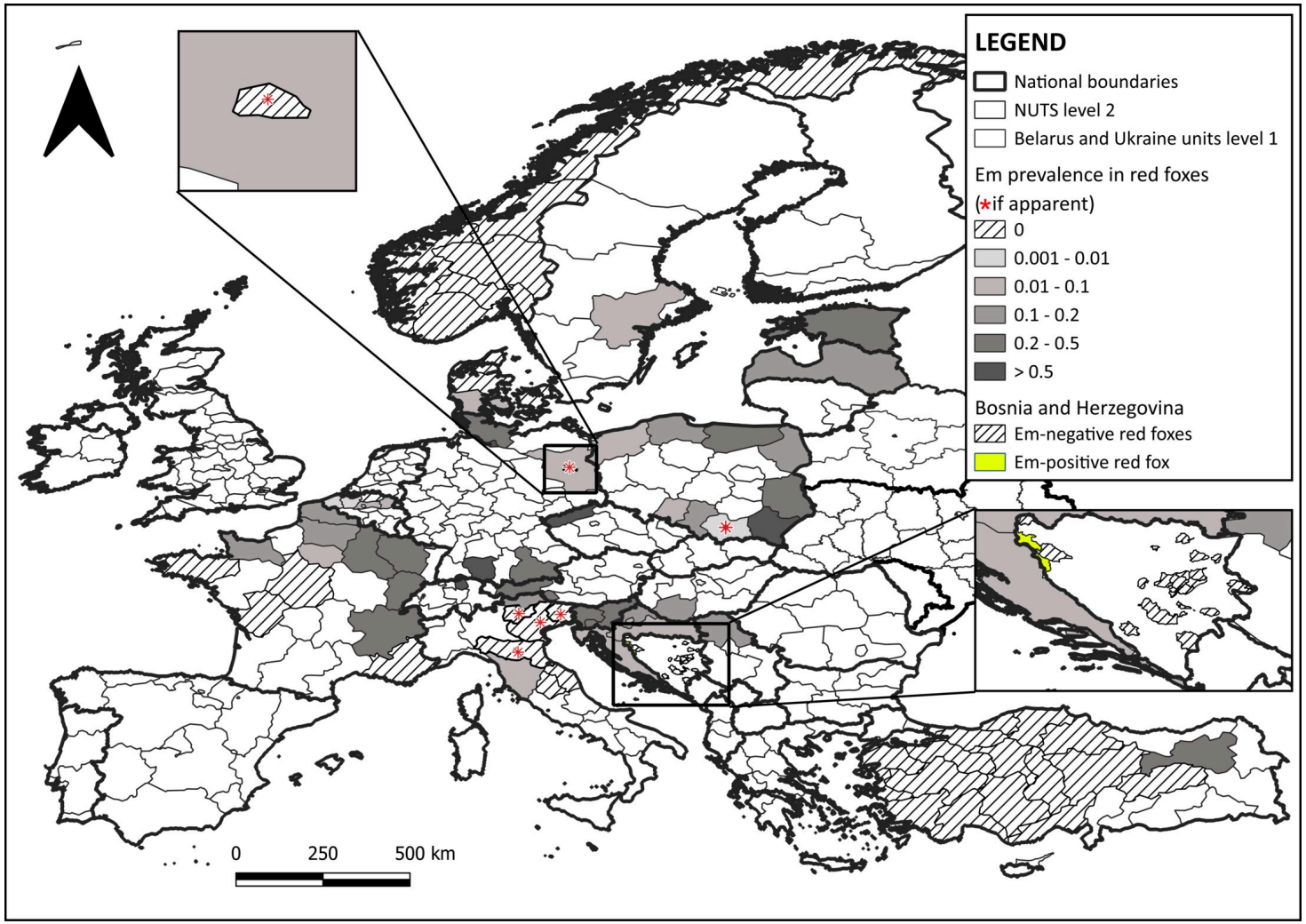
★ FIRST IN FOXES

Bosnia & Herzegovina · central Italy · Serbia

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NUTS 1 → NUTS 2

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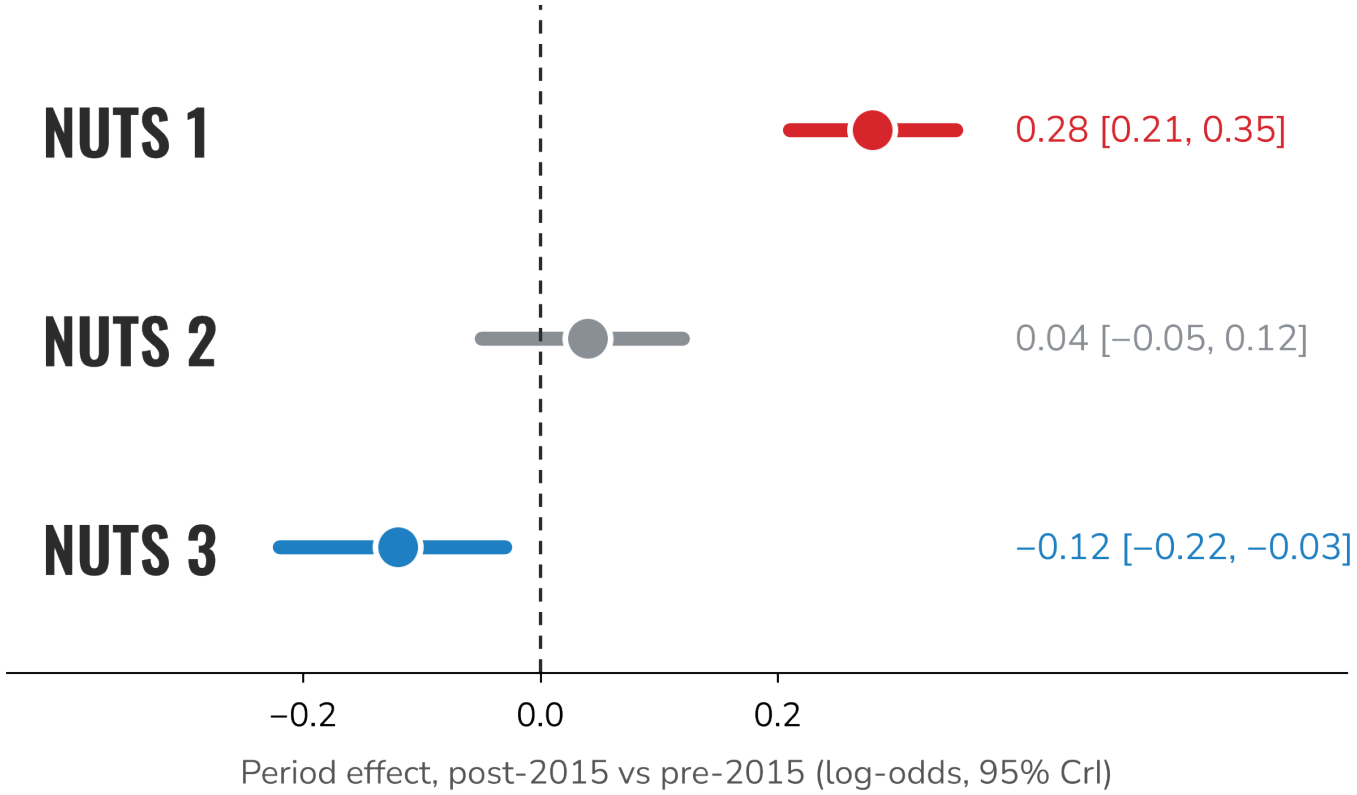
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IS PREVALENCE RISING? IT DEPENDS ON THE SCALE YOU LOOK AT

Cafiero et al. 2026, Parasit Vectors (Table 3)

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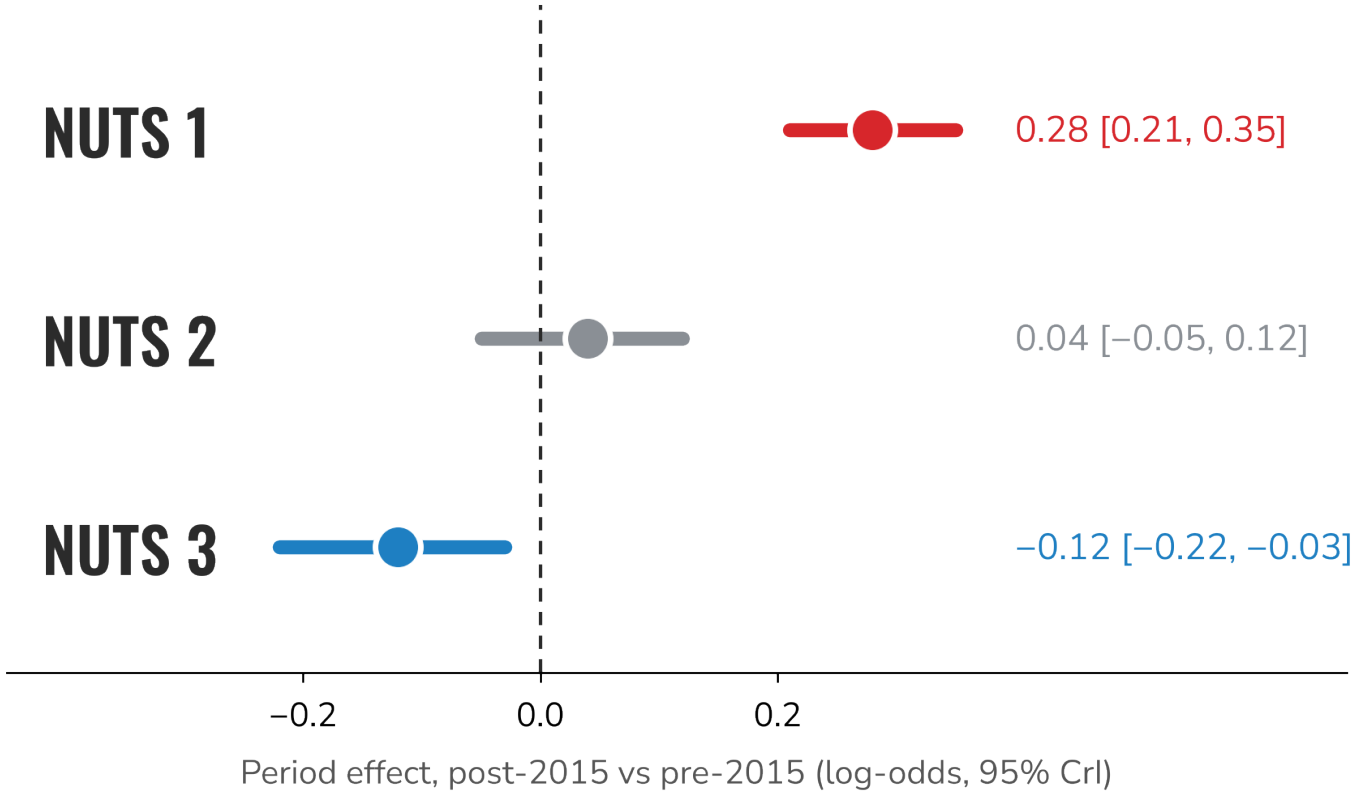


Bayesian GLMMs on red-fox positivity, pre- vs post-2015, fitted separately at each NUTS level

Cafiero et al. 2026, Parasit Vectors (Table 3)

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IS PREVALENCE RISING? IT DEPENDS ON THE SCALE YOU LOOK AT



NUTS 1 **HIGHER**

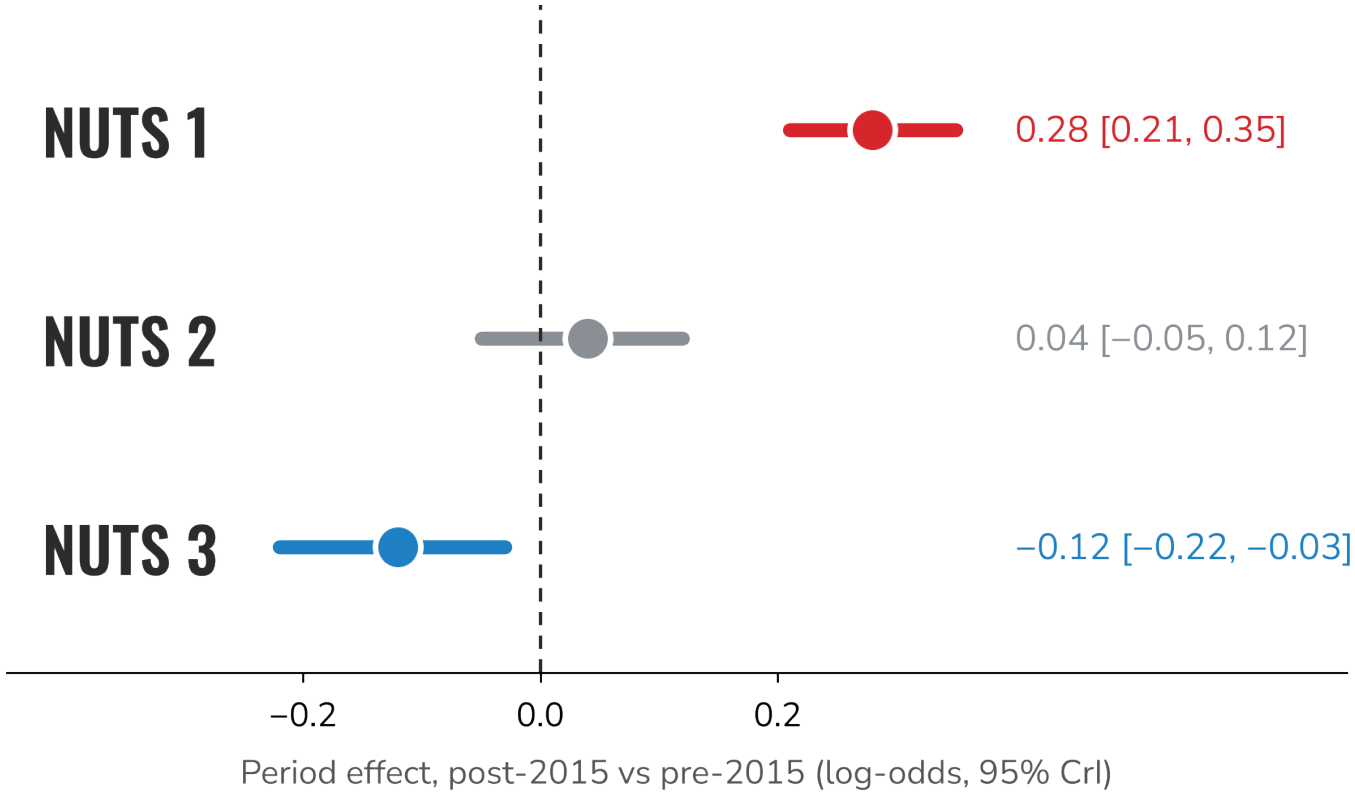
Probability of an increase > 0.99

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IS PREVALENCE RISING? IT DEPENDS ON THE SCALE YOU LOOK AT



NUTS 1 — **HIGHER**

Probability of an increase > 0.99

NUTS 2 — **NO CHANGE**

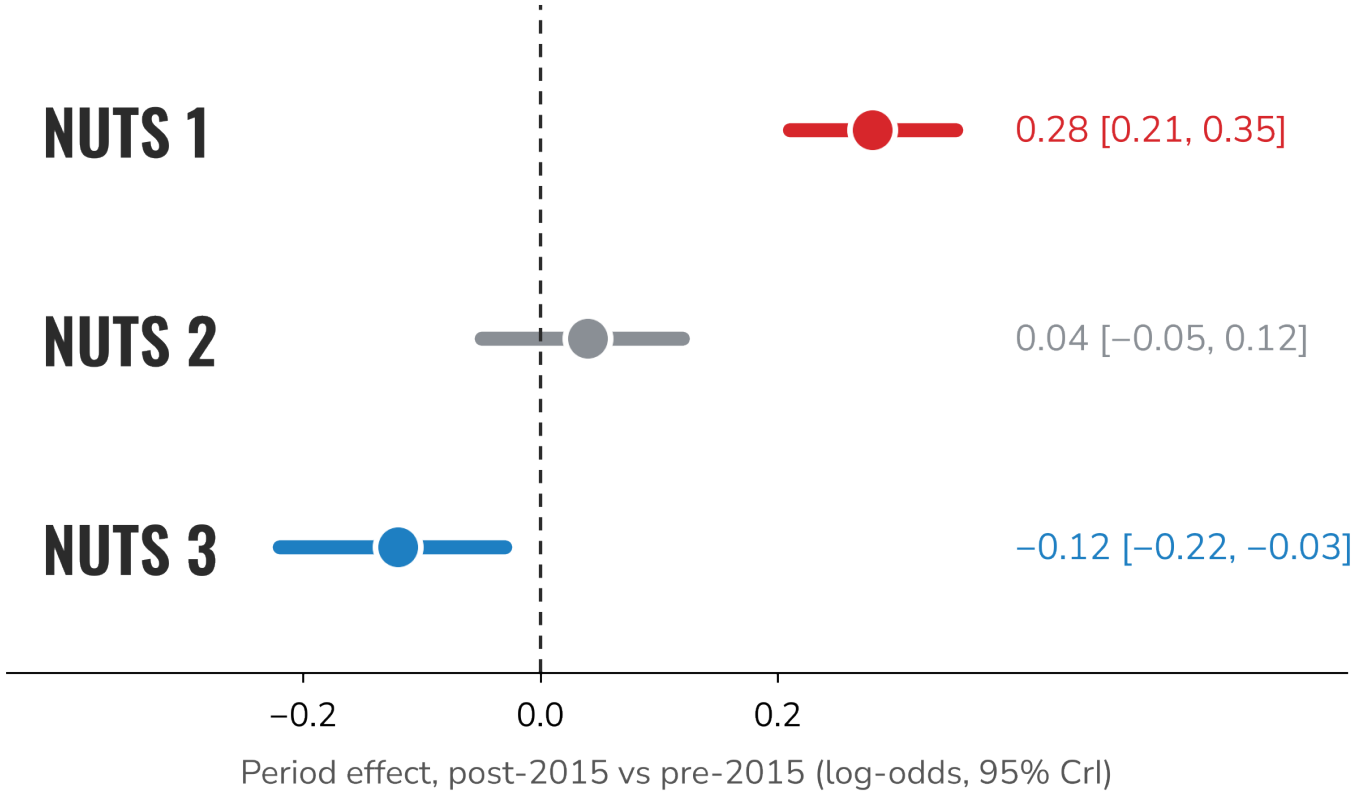
Probability of an increase 0.81 — inconclusive

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IS PREVALENCE RISING? IT DEPENDS ON THE SCALE YOU LOOK AT



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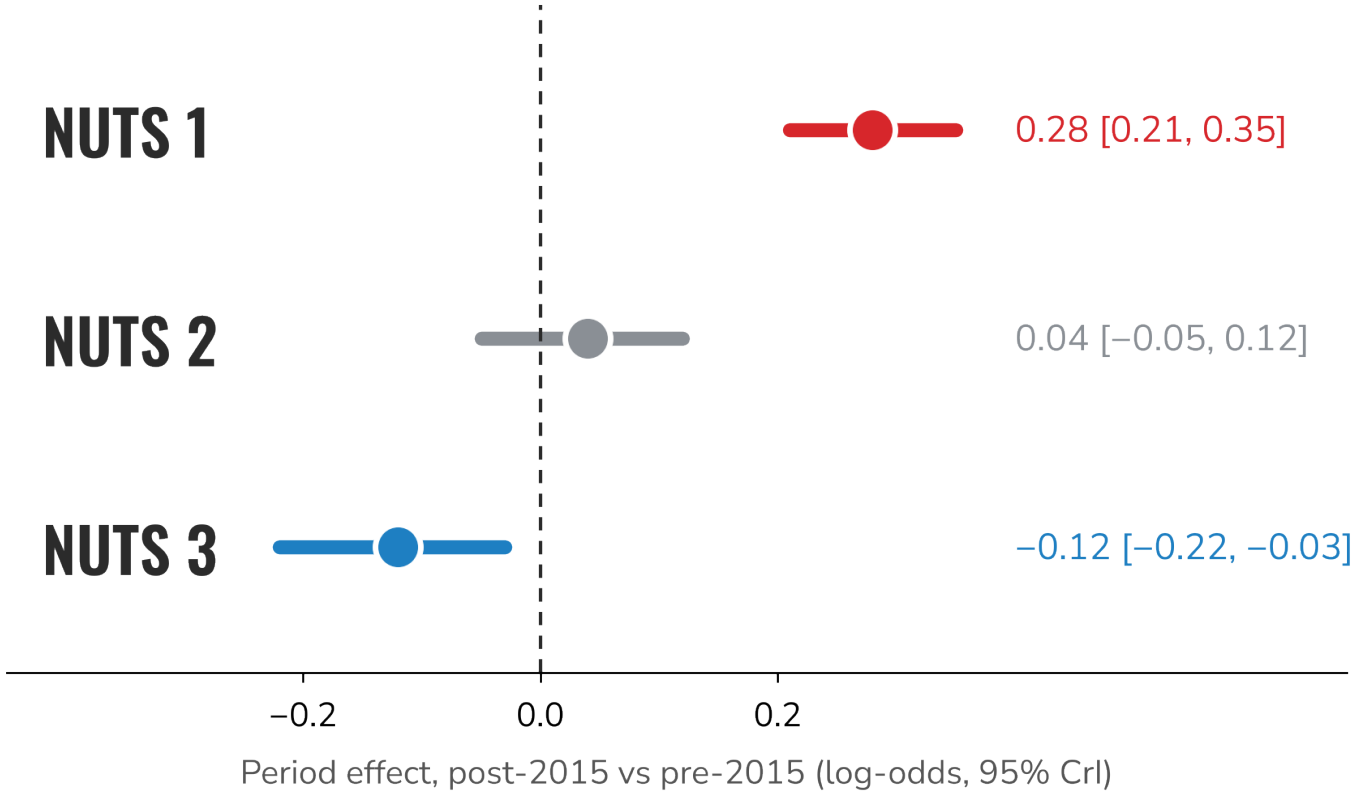
NUTS 3 — **LOWER**
Probability of a decrease 0.99

Bayesian GLMMs on red-fox positivity, pre- vs post-2015, fitted separately at each NUTS level

Cafiero et al. 2026, Parasit Vectors (Table 3)

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IS PREVALENCE RISING? IT DEPENDS ON THE SCALE YOU LOOK AT



Bayesian GLMMs on red-fox positivity, pre- vs post-2015, fitted separately at each NUTS level

NUTS 1 **HIGHER**

Probability of an increase > 0.99

NUTS 2 **NO CHANGE**

Probability of an increase 0.81 – inconclusive

NUTS 3 **LOWER**

Probability of a decrease 0.99

SAME DATA, THREE ANSWERS: BROAD-SCALE RISE ≠ LOCAL RISE

Cafiero et al. 2026, Parasit Vectors (Table 3)

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MORE HOSTS IN THE GAME

Cafiero et al. 2026, Parasit Vectors

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MORE HOSTS IN THE GAME

GOLDEN JACKAL

Bosnia & Herzegovina · Croatia · southern Hungary · Serbia · Slovenia

GREY WOLF

SE France · central Italy · Slovakia

RACCOON DOG

Denmark · Estonia

DOGS & CATS

Dogs: France · Italy · Poland · Turkey;
Cats: France · Poland

First true-prevalence estimates 2015–2025 · Cafiero et al. 2026, Parasit Vectors

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NEW DEFINITIVE HOSTS

wildcat · lynx · badger

NEW INTERMEDIATE HOSTS

Harting's vole · Persian vole · Macedonian mouse · brown hare

First true-prevalence estimates 2015–2025 · Cafiero et al. 2026, Parasit Vectors

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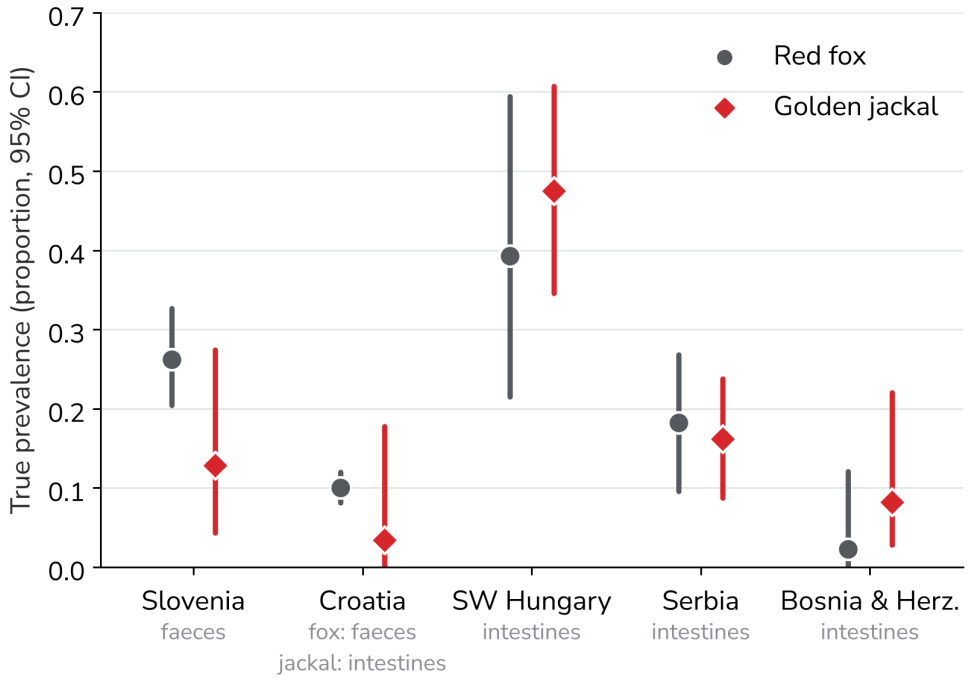
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NEW INTERMEDIATE HOSTS

Harting's vole · Persian vole · Macedonian mouse · brown hare

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GOLDEN JACKAL vs RED FOX · TRUE PREVALENCE



Sources – Slovenia: Bandelj et al. 2022, Animals · Croatia: fox, Beck et al. 2018, Parasitol Res & Balen Topić et al. 2023, Life; jackal, Sindičić et al. 2018, Acta Parasitol · SW Hungary (Baranya): Moloi et al. 2023, Sci Rep · Serbia (Vojvodina): Lalošević et al. 2016, Eur J Wildl Res · Bosnia & Herzegovina: fox, Omeragić et al. 2022, IJP-PAW; jackal, Kapo et al. 2025, IJP-PAW. True prevalence and Blaker 95% CI as estimated in Cafiero et al. 2026, Parasit Vectors

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MORE HOSTS IN THE GAME

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GREY WOLF

SE France · central Italy · Slovakia

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wildcat · lynx · badger

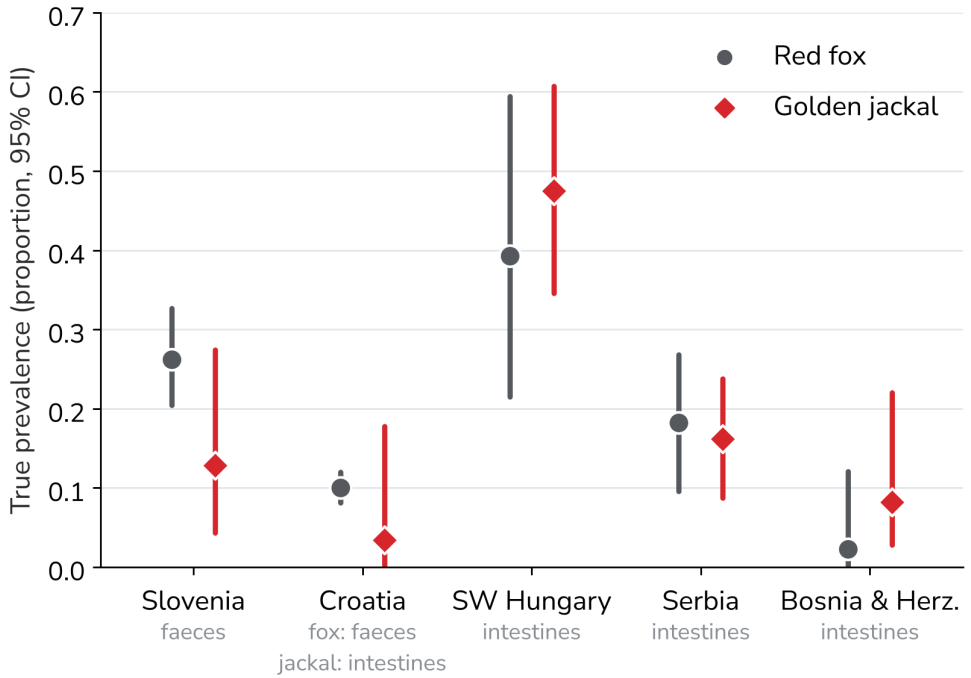
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SURVEILLANCE ON FOXES ALONE MISSES PART OF THE CYCLE

GOLDEN JACKAL vs RED FOX · TRUE PREVALENCE



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THE SOUTHERN EDGE IS MOVING

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THE SOUTHERN EDGE IS MOVING

2018 · MARITIME ALPS

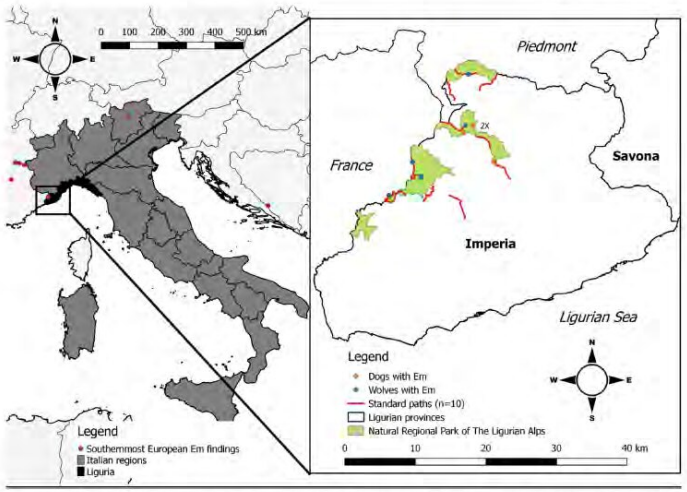


Fig. 1. Locations of wolf (blue dots) and dog (orange dots) fecal samples positive to *Echinococcus multilocularis* collected during a survey on *Echinococcus* spp. carried out from June to November 2017 in a mountainous area in the Alps of the Imperia Province, Italy. In the map are also reported the southernmost reports of *Echinococcus multilocularis* (*E. multilocularis*) to date in Europe (France, Drs. Boué and Umhang, pers. communication; North-Eastern Italian Alps, Croatia, as in (Beck et al., 2018)). Two dog fecal samples were collected from the same pasture and are represented by a single dot (noted as 2×). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Em eggs in faeces of wolves (5/120) and shepherd dogs (4/30) – apparent, ~130 km south of the southernmost Alpine record

Massolo et al. 2018, IJP-PAW

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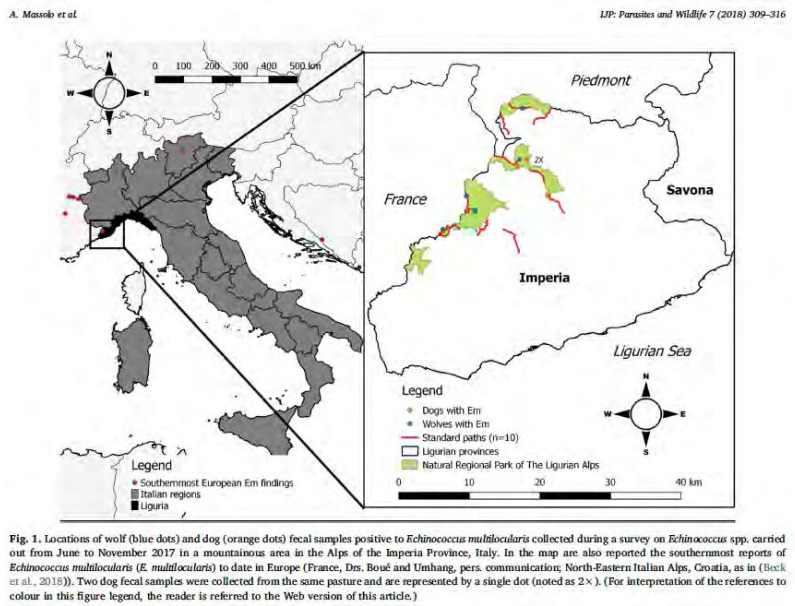


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2022–2025 · ALTO ADIGE

HIGHLY ENDEMIC

Red foxes re-assessed, 2019–2020

Obber et al. 2022, PLoS ONE

Microtus arvalis: 116/142 rodent prey in fox stomachs; *Em* in 3/85 voles – 0.035 (95% CI 0.008–0.103), apparent, PCR on tissues

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THE SOUTHERN EDGE IS MOVING

2018 · MARITIME ALPS

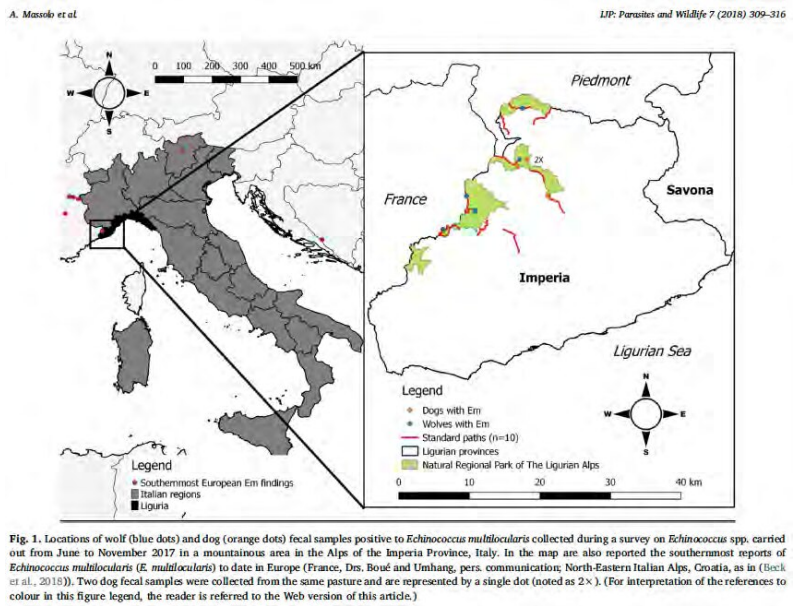


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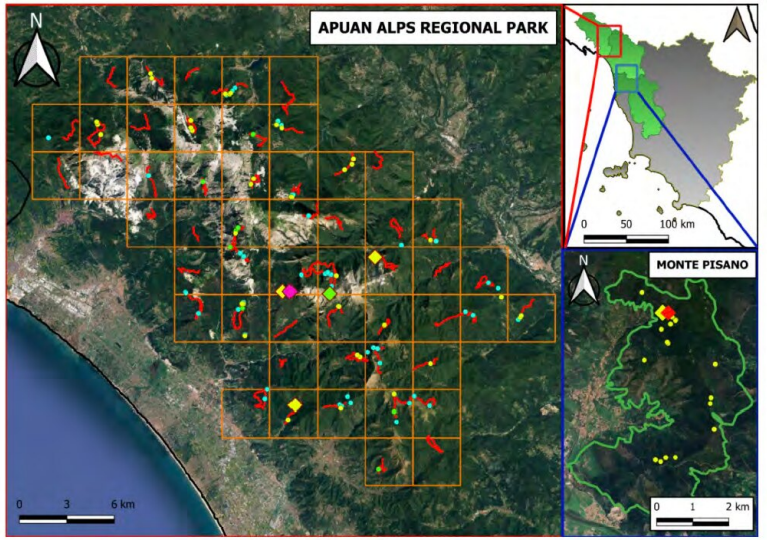
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2025 · NORTHERN APENNINES



Apuan Alps & Monte Pisano: *Em* eggs (single-egg PCR) in faeces of wolves and red foxes

Cafiero et al. 2025, Sci Rep

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THE SOUTHERN EDGE IS MOVING

2018 · MARITIME ALPS

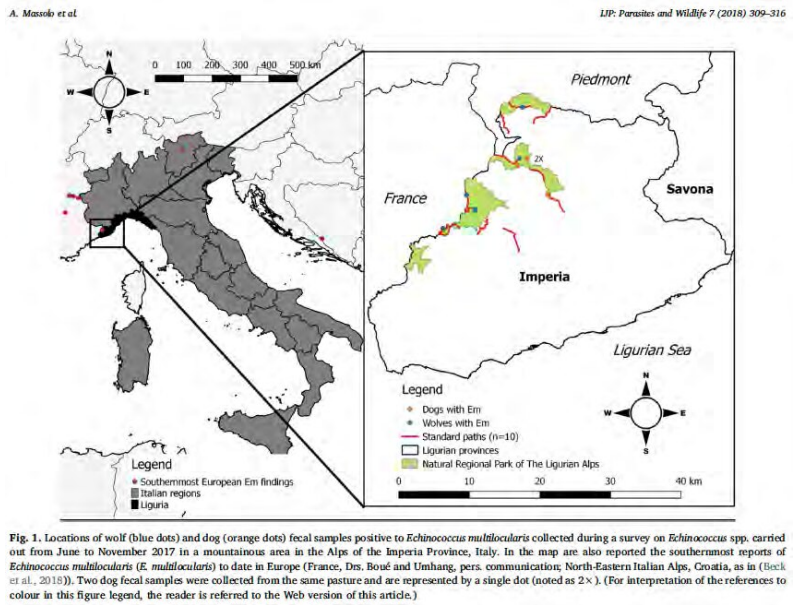


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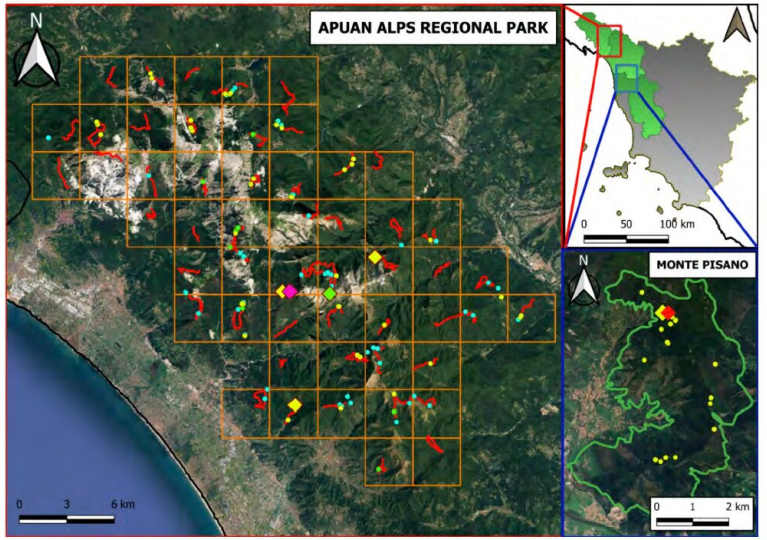
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2025 · NORTHERN APENNINES



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Cafiero et al. 2025, Sci Rep

A FEW HUNDRED KM FROM THE NEAREST KNOWN FOCUS

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TAKE-HOME

THE PATTERN

TAKE-HOME

THE PATTERN

Expansion is real — but scale-dependent

TAKE-HOME

THE PATTERN

Expansion is real — but scale-dependent

More regions, more hosts, new southern edges

TAKE-HOME

THE PATTERN

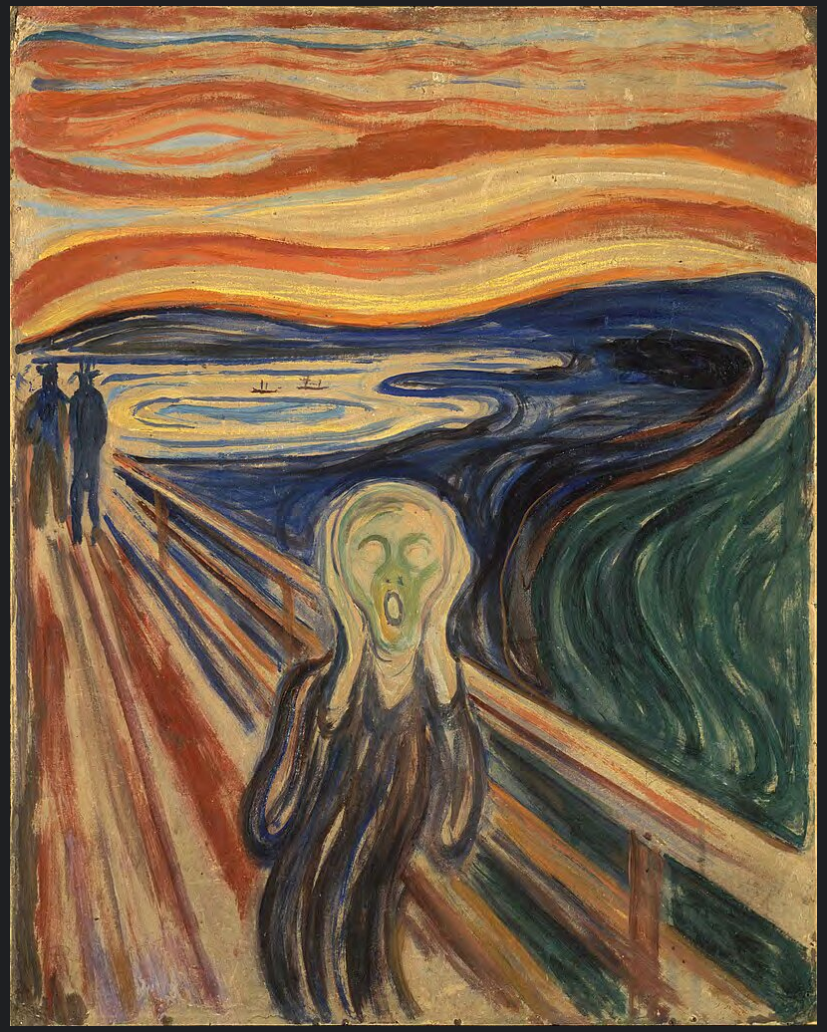
- Expansion is real — but scale-dependent
- More regions, more hosts, new southern edges
- Part of the 'new' is new sampling

II

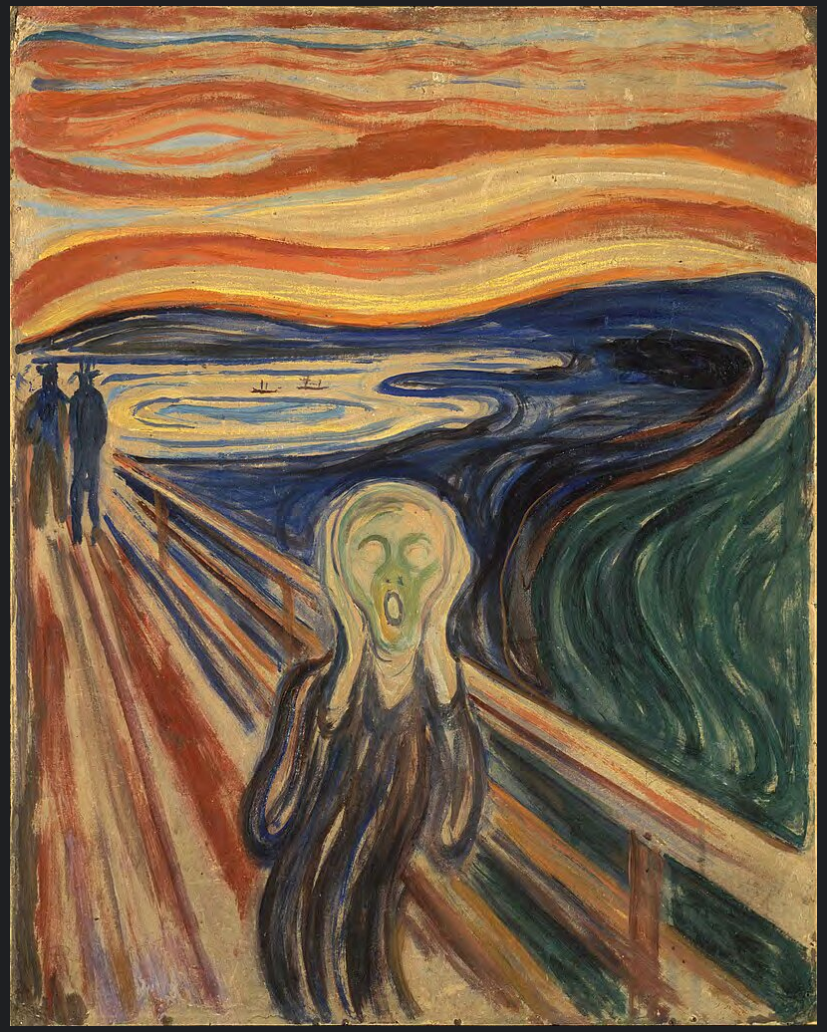
FROM PATTERN TO PROCESS

Why here, why now – and why not there?



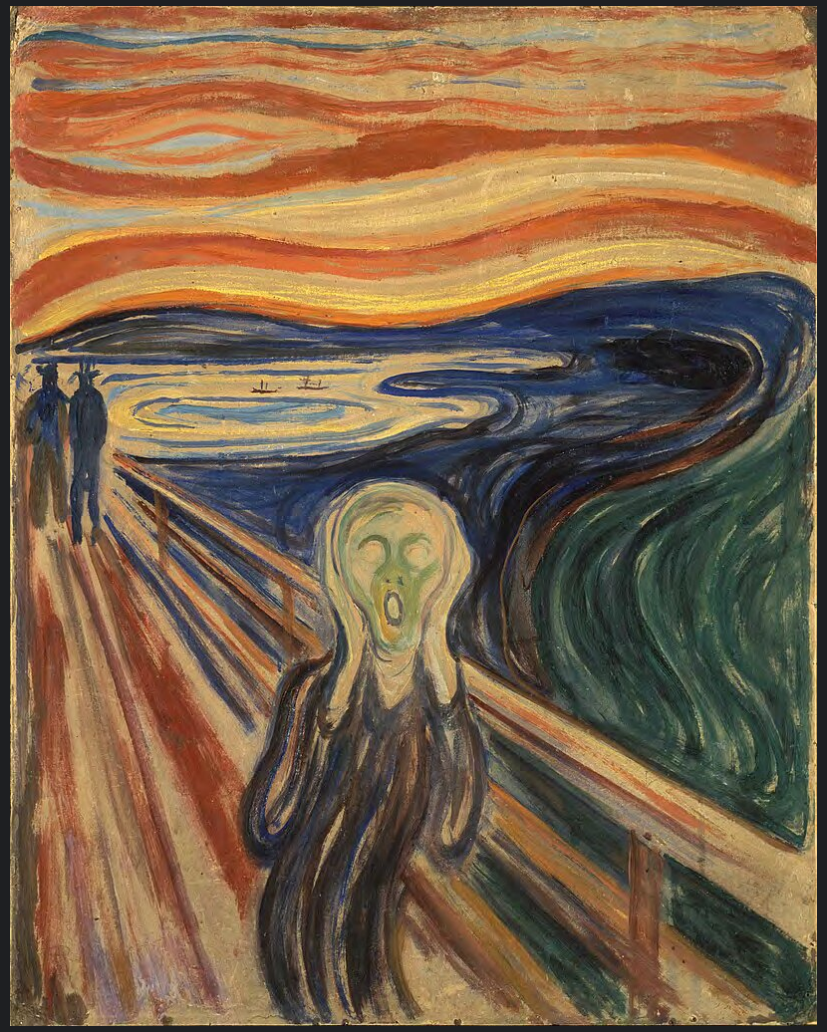


One or more definitive hosts · one or more intermediate hosts · differential susceptibility and competence · egg survival · encounter rates · dilution by non-hosts · competitors and predators · climate · land use · people



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One or more definitive hosts · one or more intermediate hosts · differential susceptibility and competence · egg survival · encounter rates · dilution by non-hosts · competitors and predators · climate · land use · people

“There is no single scale at which ecological phenomena should be studied”

Patterns emerge “from the collective behavior of large ensembles of smaller scale units”

Levin 1992, Ecology

PROCESSES NEST ACROSS SCALES — IN SPACE AND IN TIME



Images: Em adult worm; common vole; Apuan Alps survey grid (Cafiero et al. 2025, Sci Rep); Maritime Alps (Massolo et al. 2018, IJP-PAW); NUTS1 red-fox true prevalence (Cafiero et al. 2026, Parasit Vectors); Em distribution vs aridity (Massolo et al. 2022, Trends Parasitol)

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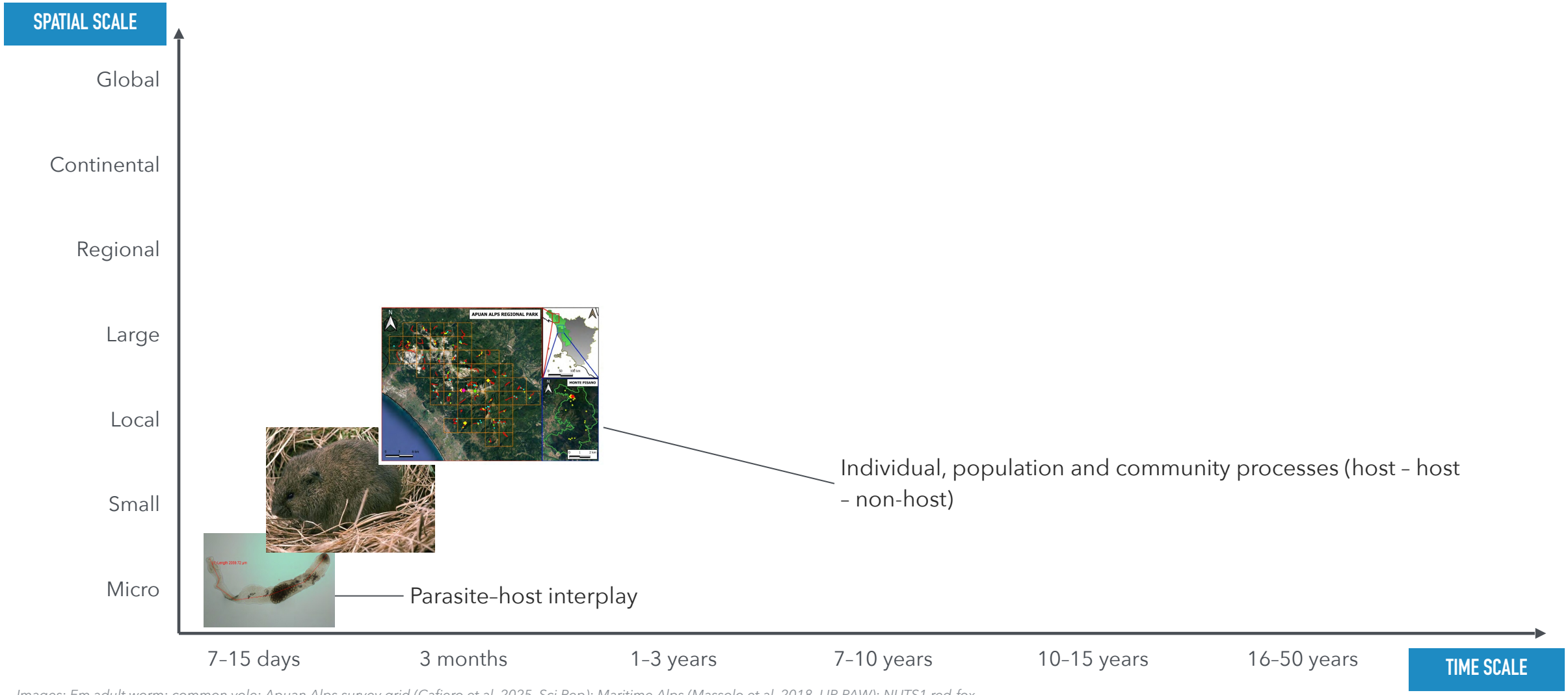
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PROCESSES NEST ACROSS SCALES — IN SPACE AND IN TIME

SPATIAL SCALE

Global

Continental

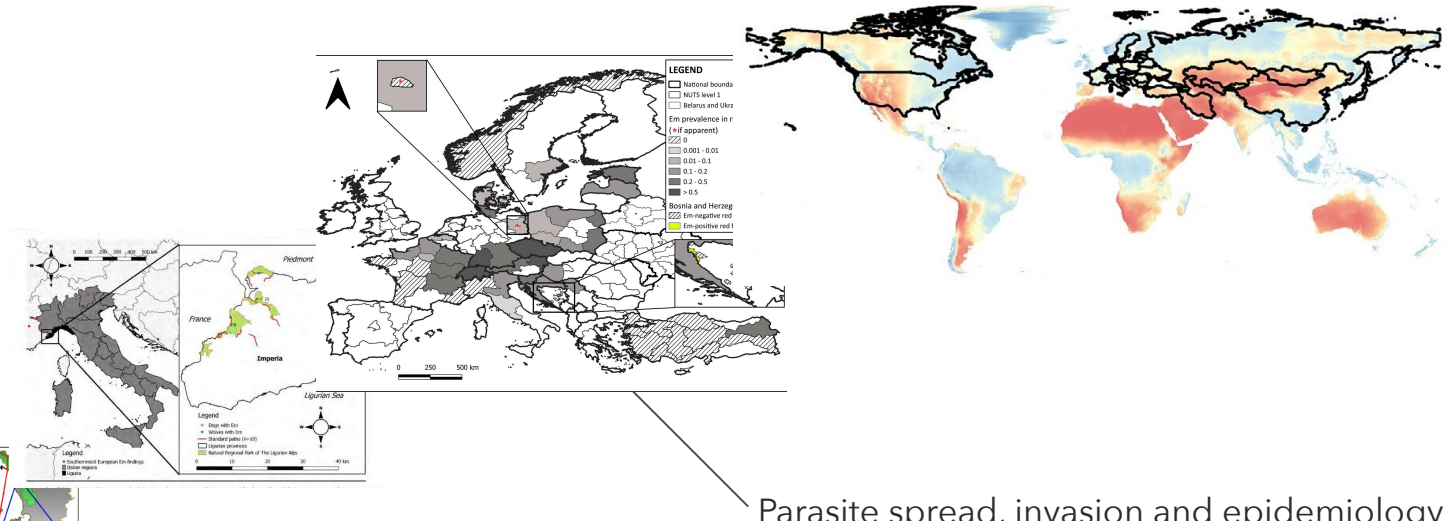
Regional

Large

Local

Small

Micro



Parasite spread, invasion and epidemiology

Individual, population and community processes (host – host – non-host)

Parasite–host interplay

7–15 days | 3 months | 1–3 years | 7–10 years | 10–15 years | 16–50 years

TIME SCALE

Images: Em adult worm; common vole; Apuan Alps survey grid (Cafiero et al. 2025, Sci Rep); Maritime Alps (Massolo et al. 2018, IJP-PAW); NUTS1 red-fox true prevalence (Cafiero et al. 2026, Parasit Vectors); Em distribution vs aridity (Massolo et al. 2022, Trends Parasitol)

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SPATIAL SCALE

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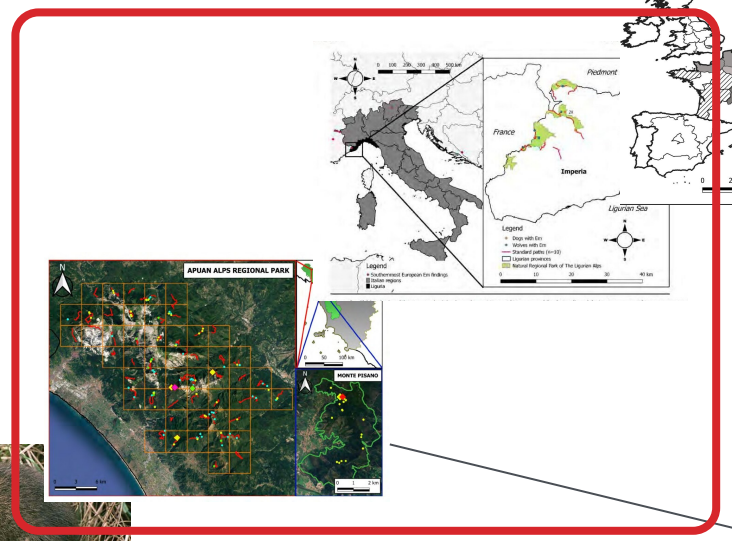
Large

Local

Small

Micro

KEY SCALE?

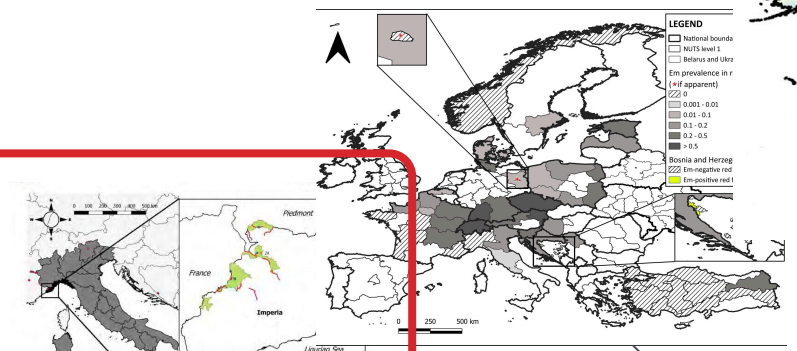


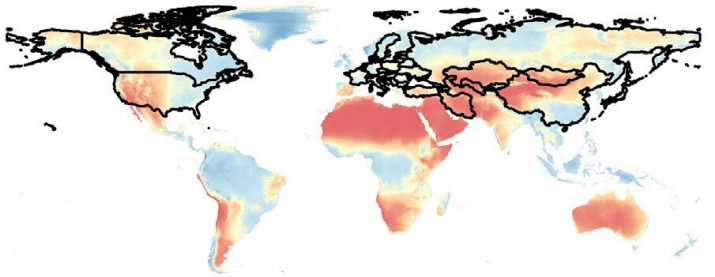




Parasite–host interplay

Individual, population and community processes (host – host – non-host)





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PROCESSES NEST ACROSS SCALES — IN SPACE AND IN TIME

SPATIAL SCALE

Global

Continental

Regional

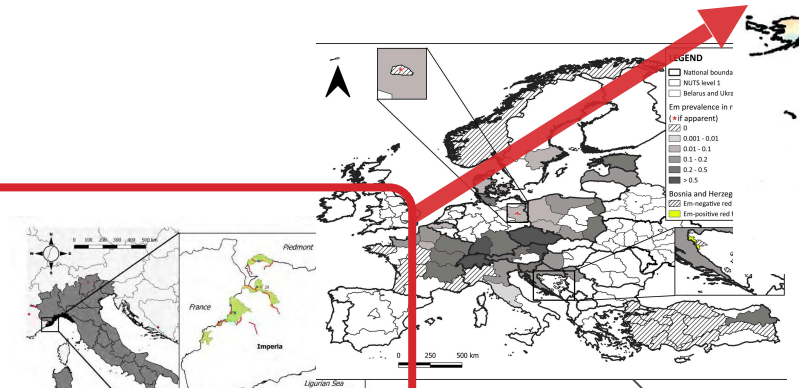
Large

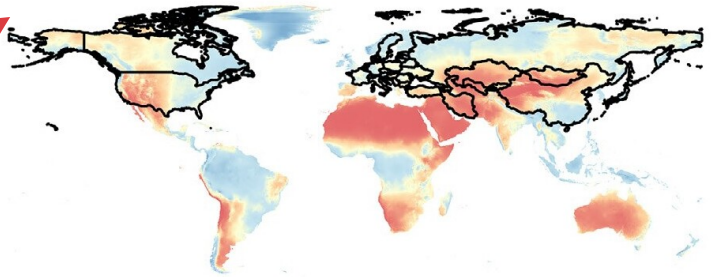
Local

Small

Micro

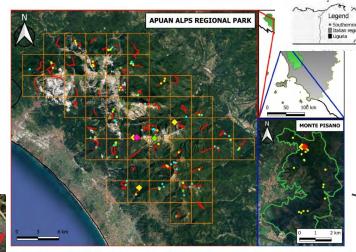
KEY SCALE?



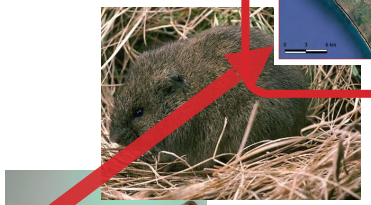


Parasite spread, invasion and epidemiology

BOTTOM-UP



Individual, population and community processes (host – host – non-host)



Parasite–host interplay

7–15 days | 3 months | 1–3 years | 7–10 years | 10–15 years | 16–50 years

TIME SCALE

Images: Em adult worm; common vole; Apuan Alps survey grid (Cafiero et al. 2025, Sci Rep); Maritime Alps (Massolo et al. 2018, IJP-PAW); NUTS1 red-fox true prevalence (Cafiero et al. 2026, Parasit Vectors); Em distribution vs aridity (Massolo et al. 2022, Trends Parasitol)

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PROCESSES NEST ACROSS SCALES — IN SPACE AND IN TIME

SPATIAL SCALE

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Continental

Regional

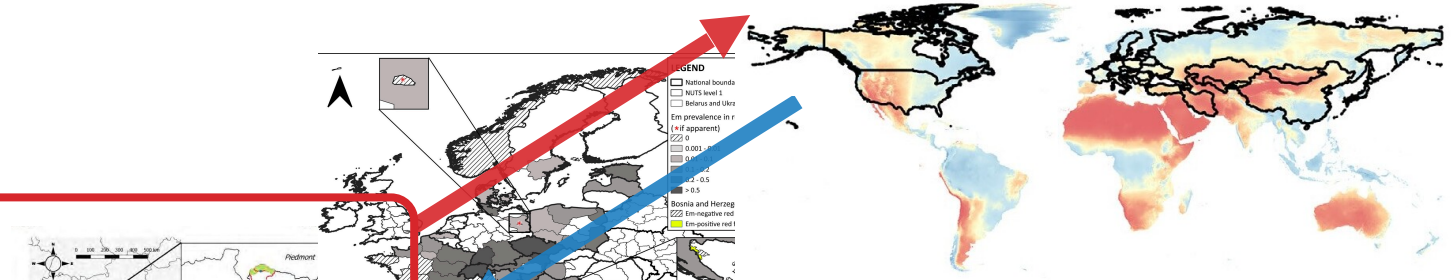
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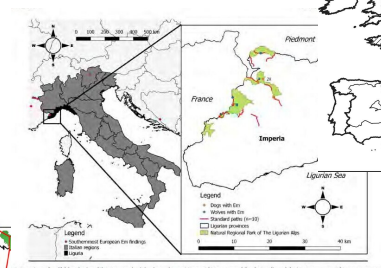
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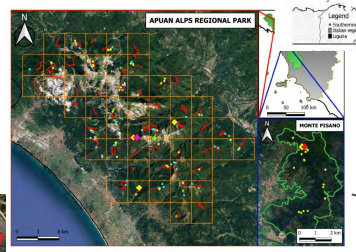
Small

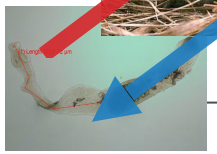
Micro

KEY SCALE?









Parasite spread, invasion and epidemiology

BOTTOM-UP **TOP-DOWN**

Individual, population and community processes (host – host – non-host)

Parasite–host interplay

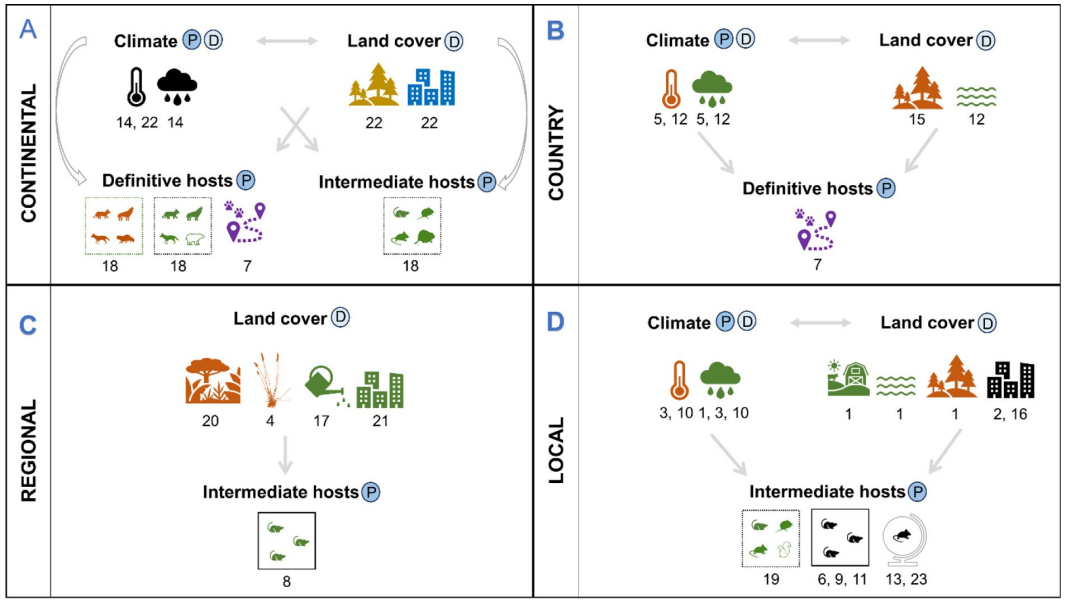
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WHAT DRIVES EM — SCALE BY SCALE



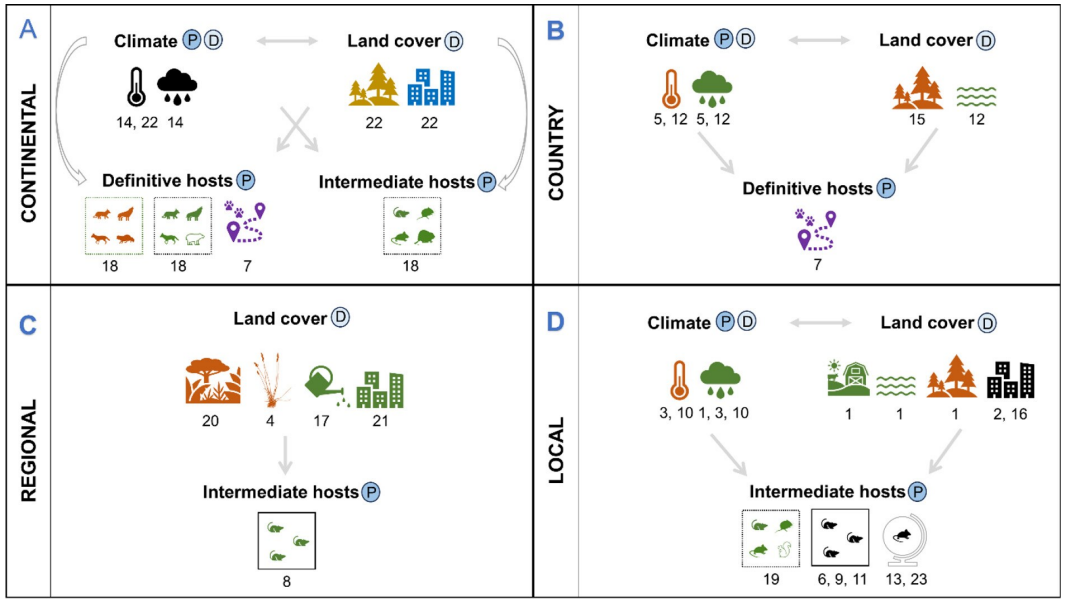
	Temperature		Pasture		DH density
	Precipitation/Humidity		Urban		DH proportion
	Water bodies		DH* dispersal		IH richness
	Kitchen gardens		IH** distribution	+ correlation	
	Natural habitat		DH density	- correlation	
	Forest		DH proportion	Unimodal	
	Grass		DH richness	Asymptotic	
				Other	
				More than one	
				P Proximal driver	
				D Distal driver	

*DH = Definitive Host, **IH = Intermediate Host

Simoncini & Massolo 2024, Food Waterborne Parasitol – systematic review, 23 studies

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WHAT DRIVES EM — SCALE BY SCALE



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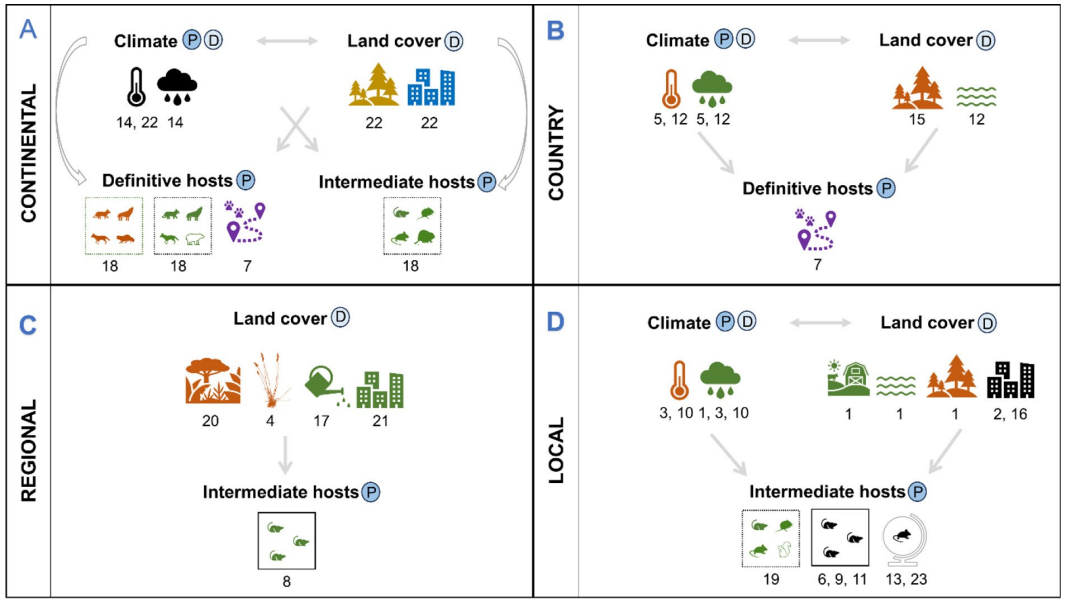
CONTINENTAL

Dispersal of definitive hosts, climate, distribution of intermediate hosts and host communities

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WHAT DRIVES EM — SCALE BY SCALE



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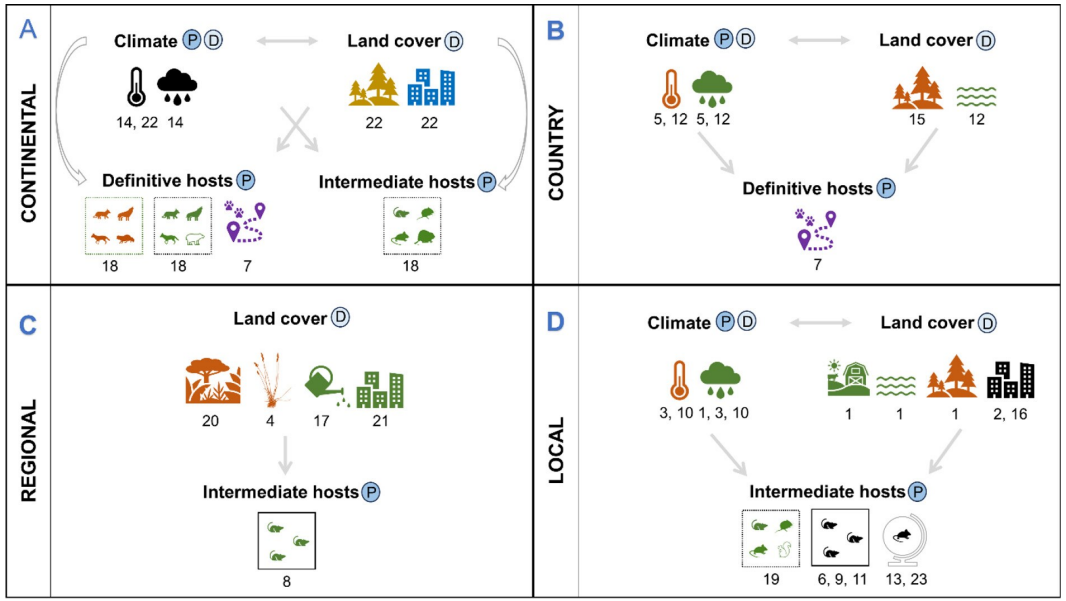
COUNTRY · REGIONAL

Climate vs land cover: their weight changes with the area considered

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WHAT DRIVES EM — SCALE BY SCALE



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CONTINENTAL

Dispersal of definitive hosts, climate, distribution of intermediate hosts and host communities

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Climate vs land cover: their weight changes with the area considered

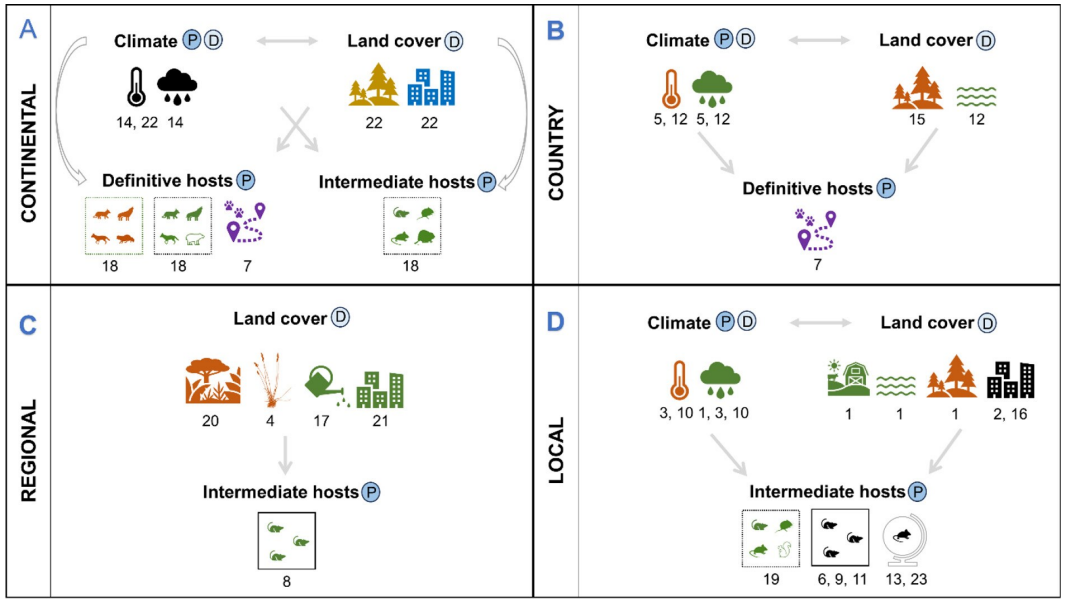
LOCAL

Trophic links between carnivores and small mammals; defecation and marking behaviour of definitive hosts

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WHAT DRIVES EM — SCALE BY SCALE



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CONTINENTAL

Dispersal of definitive hosts, climate, distribution of intermediate hosts and host communities

COUNTRY · REGIONAL

Climate vs land cover: their weight changes with the area considered

LOCAL

Trophic links between carnivores and small mammals; defecation and marking behaviour of definitive hosts

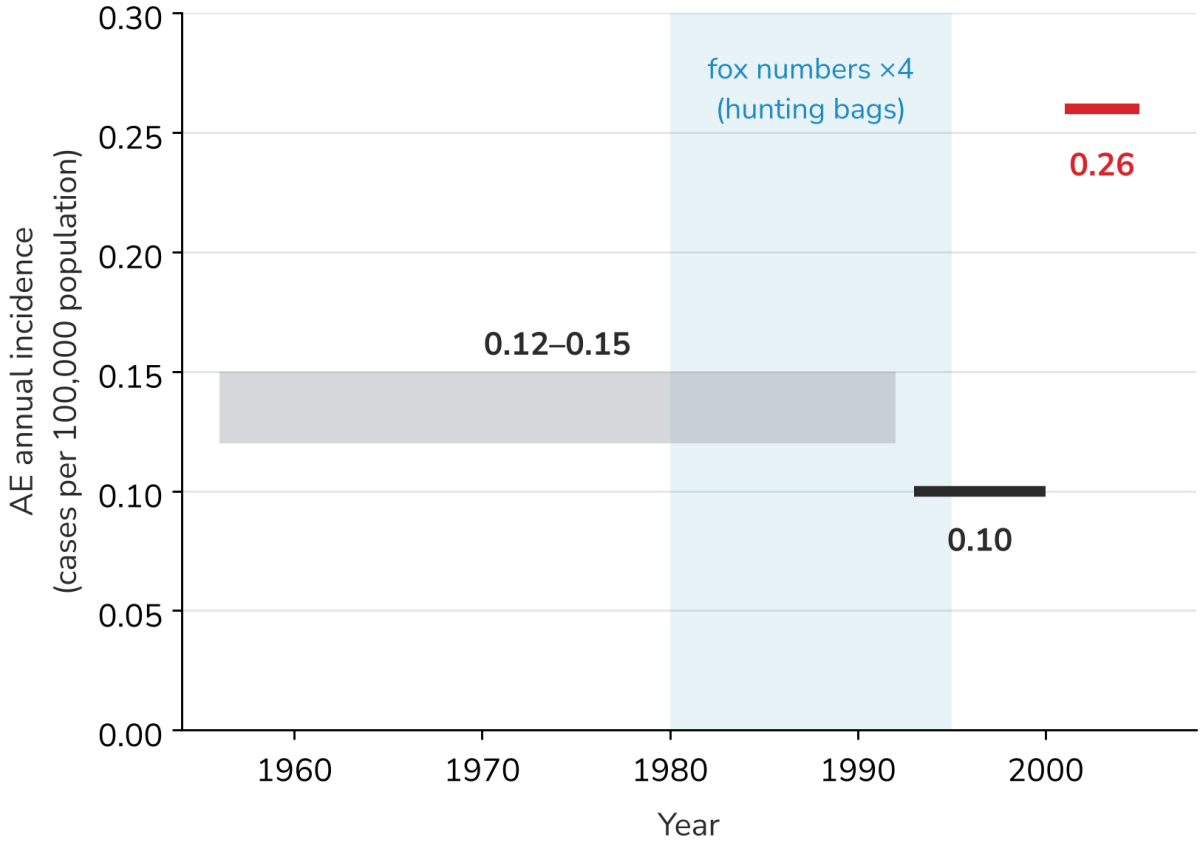
NO DRIVER IS UNIVERSAL — ITS EFFECT DEPENDS ON SCALE

Simoncini & Massolo 2024, Food Waterborne Parasitol – systematic review, 23 studies

A Massolo, Dept. Biology, Univ. Pisa | alessandro.massolo@unipi.it

DRIVER 1 · MORE FOXES, MORE HUMAN CASES — A DECADE LATER

HUMAN AE INCIDENCE, SWITZERLAND

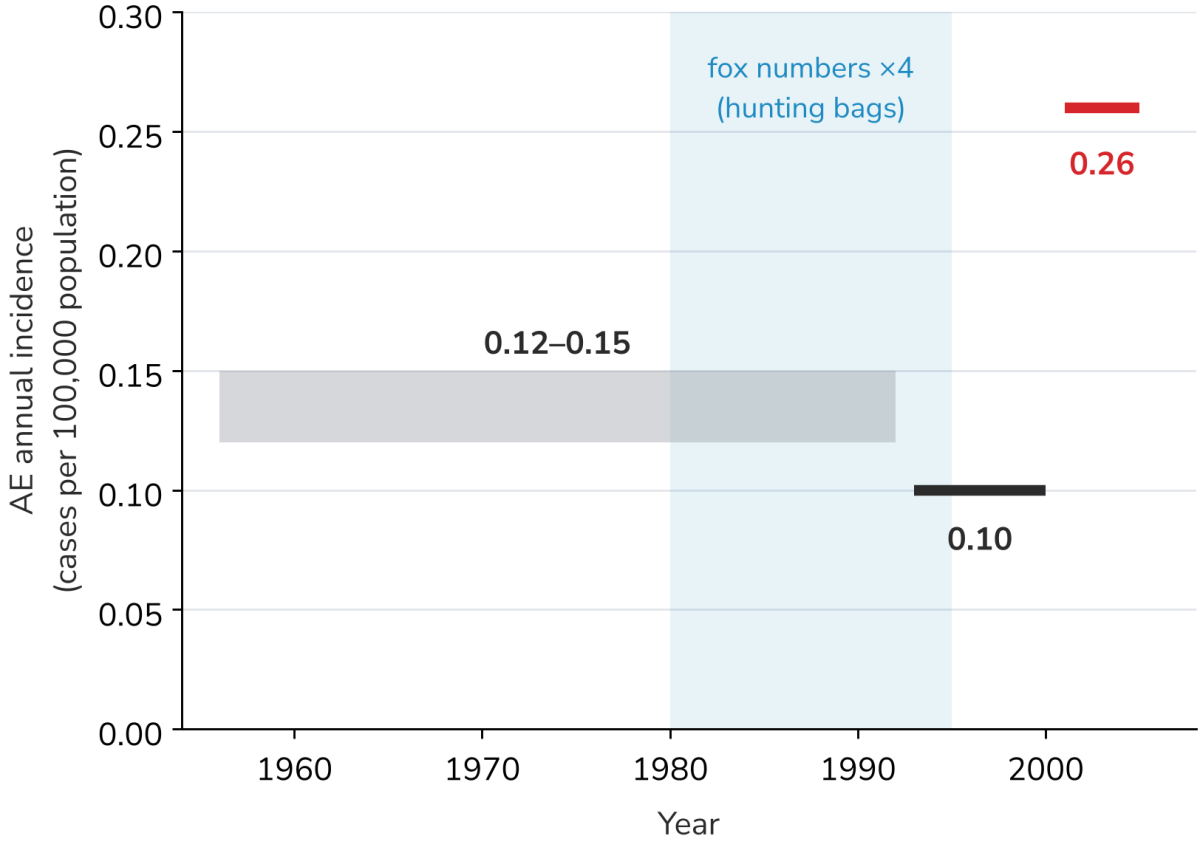


Schweiger et al. 2007, Emerg Infect Dis – mean annual incidence per period, 494 cases from case-finding studies and the 3 Swiss treatment centres; 1956–1992 shown as the range of period estimates

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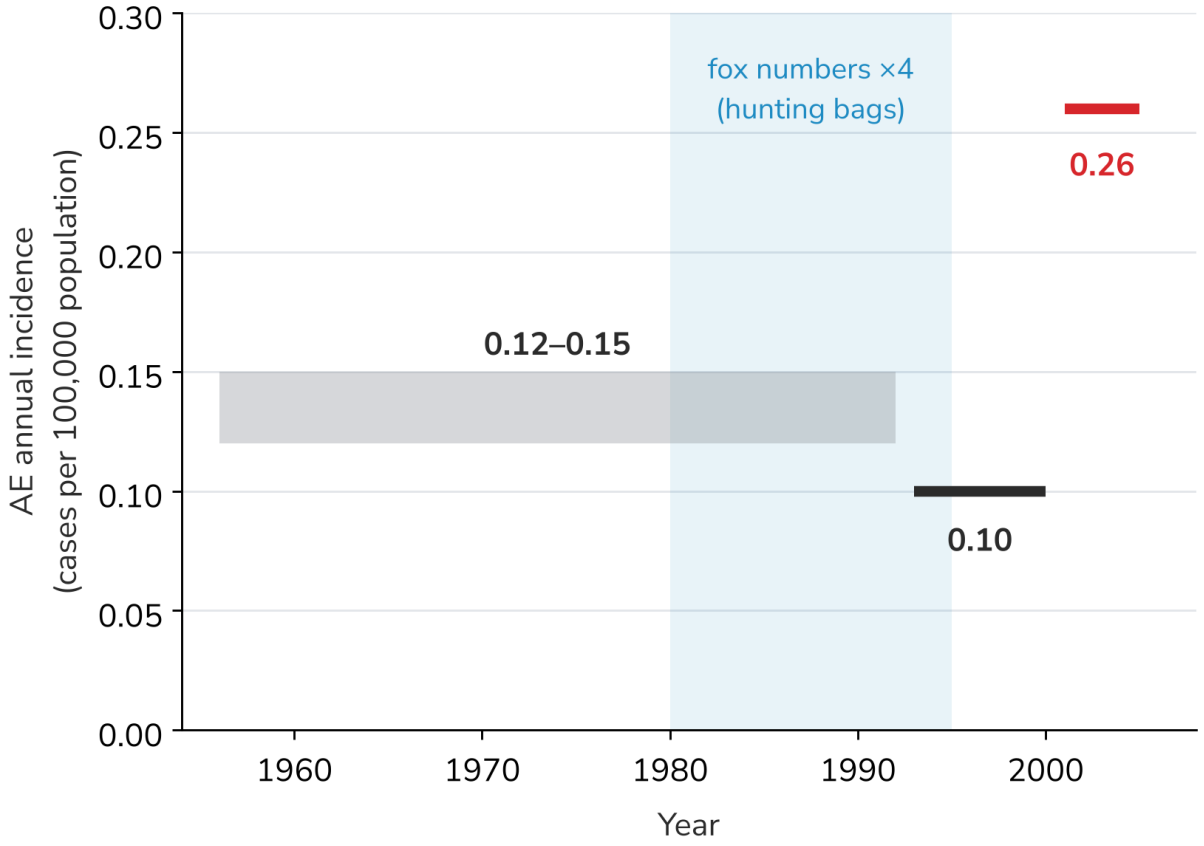
Swiss fox population 1980→1995 (hunting statistics), after oral rabies vaccination

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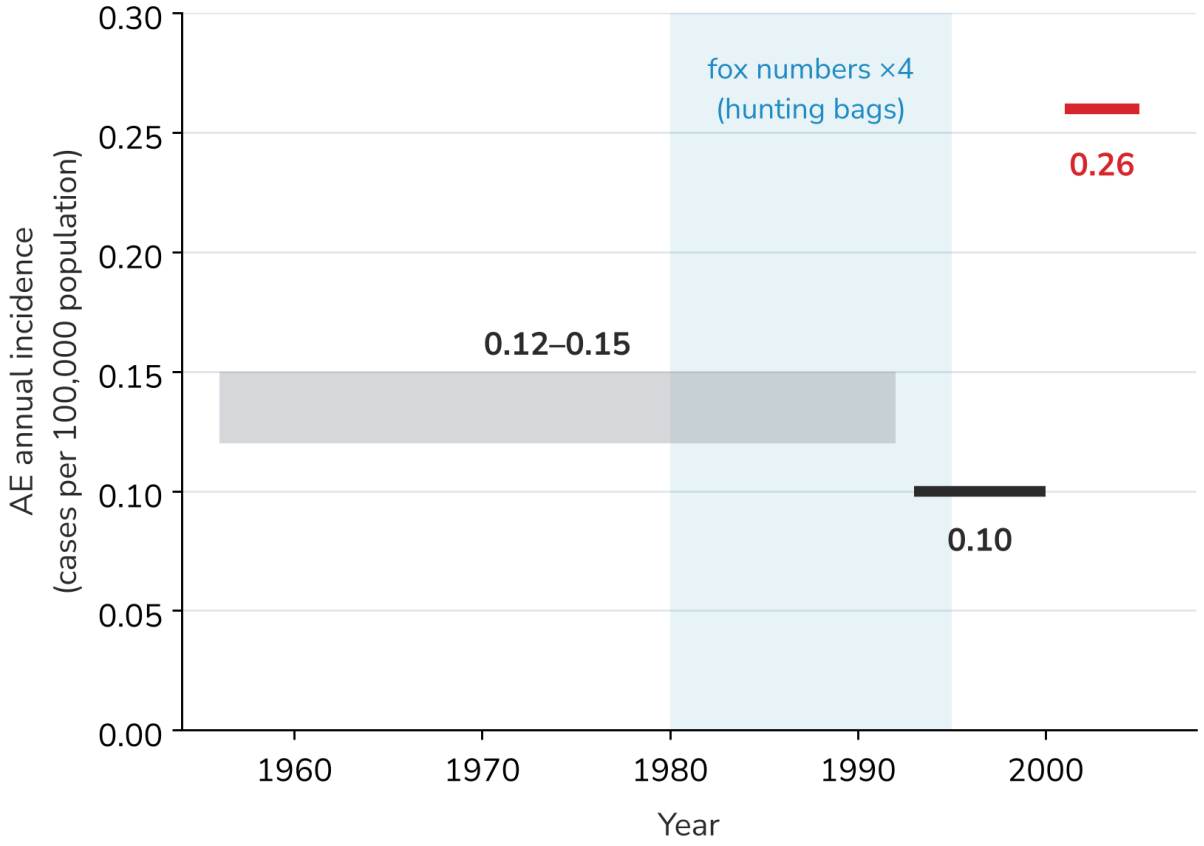
Rabies vaccination · loss of top predators · feeding · tameness → foxes colonise towns

Hegglin et al. 2015, Trends Parasitol

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AE INCIDENCE FOLLOWS FOXES WITH A 10–15-YEAR LAG

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DRIVER 2 · . . .BUT FOXES ARE NOT ENOUGH: THE RIGHT PREY



Common vole · Microtus arvalis

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DRIVER 2 · . . .BUT FOXES ARE NOT ENOUGH: THE RIGHT PREY



Common vole · Microtus arvalis

TICINO, SOUTH OF THE ALPS

22

years of a stable endemic border (404 necropsied foxes + 79 fox faeces) – matching the range of the common vole, not of the fox

Guerra et al. 2014, Parasitology

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ALTO ADIGE, ITALY

0.82

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Cafiero et al. 2025, IJP-PAW

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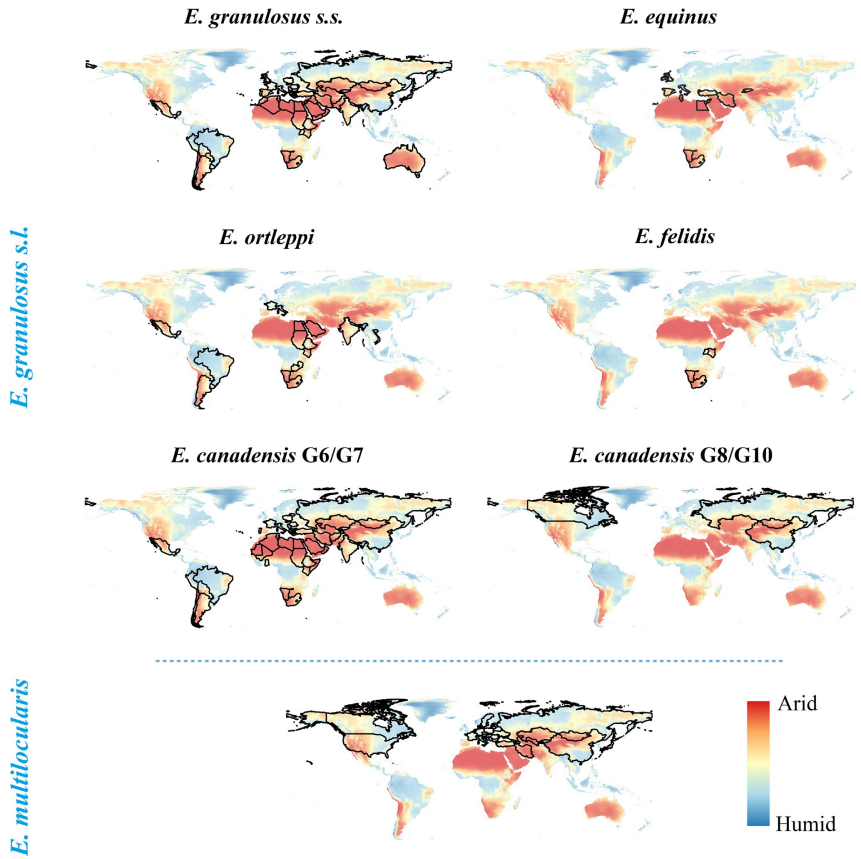
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FOX DENSITY IS NECESSARY, NOT SUFFICIENT

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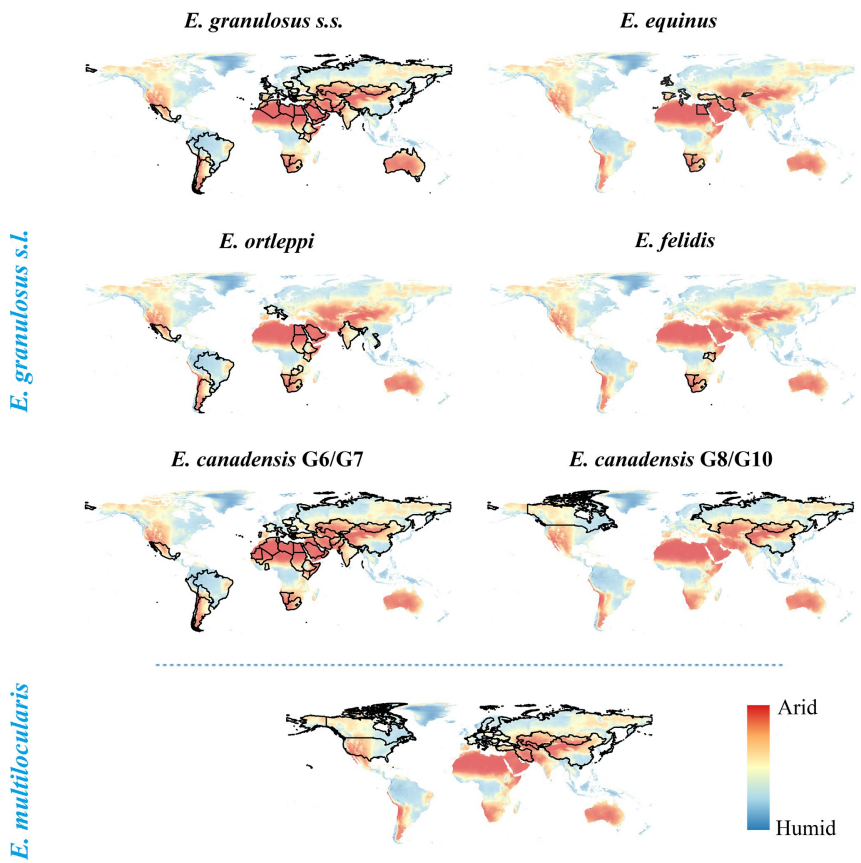
WHY HOLARCTIC ONLY? THE 'BRIDGE EFFECT'

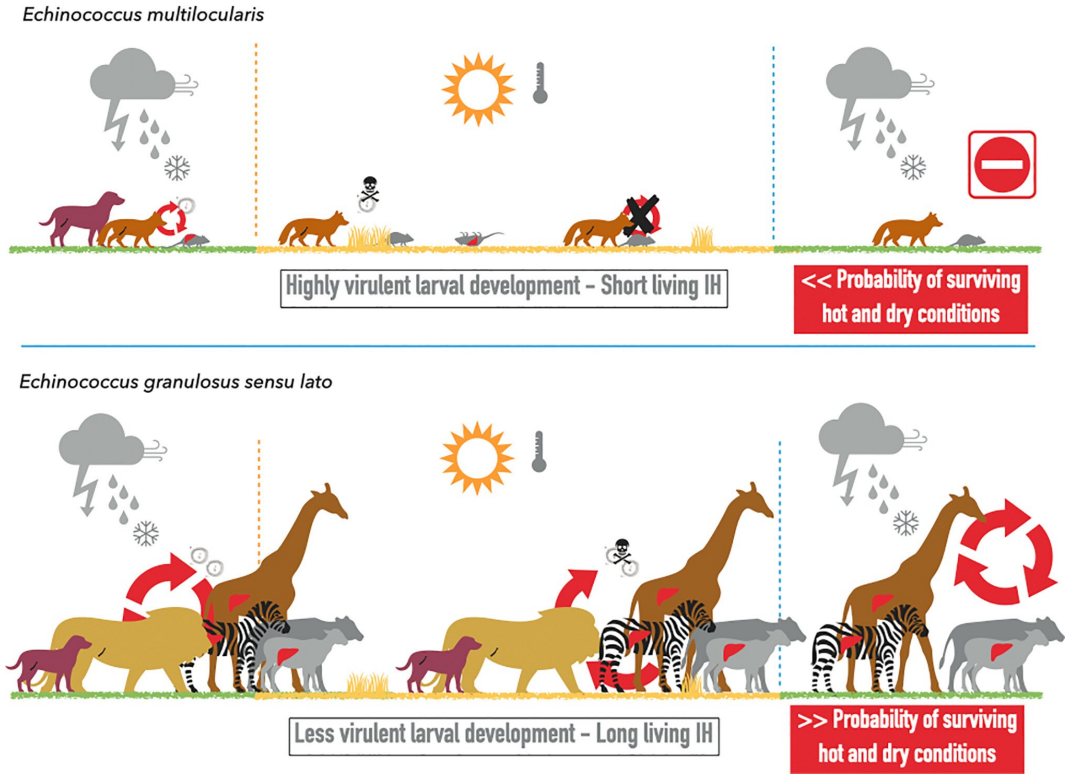


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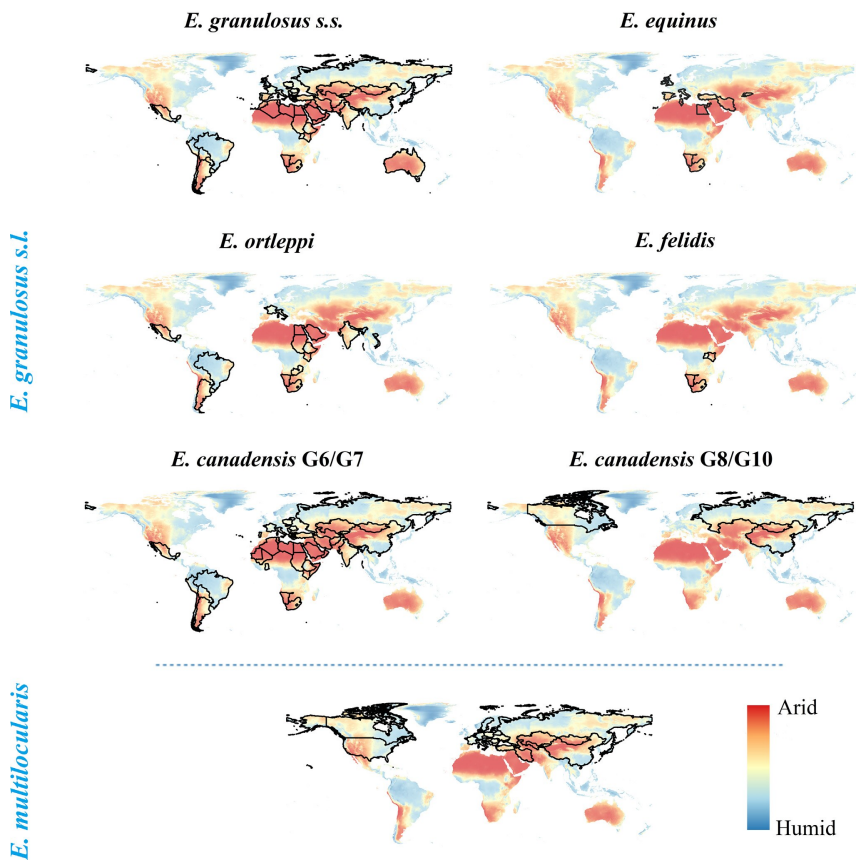


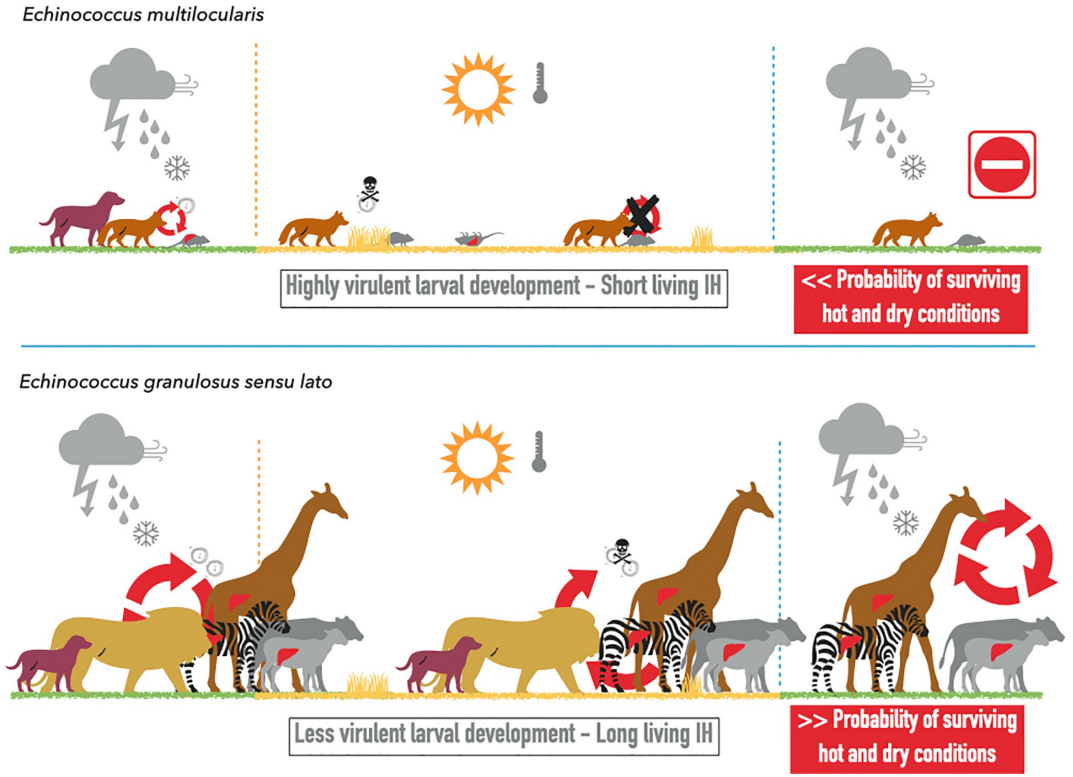


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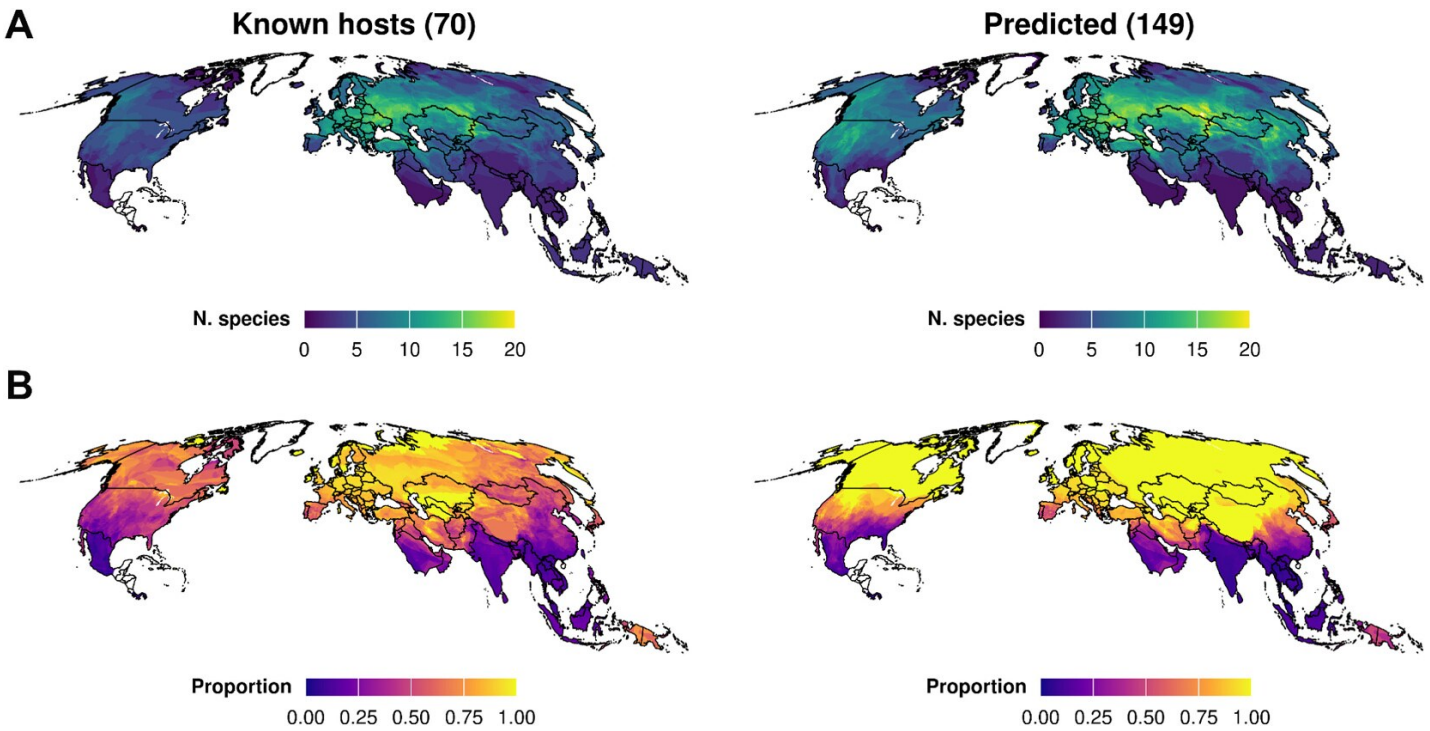


HIGHLY VIRULENT IN SHORT-LIVED PREY → NO BRIDGE ACROSS HOT, DRY LANDSCAPES

Massolo et al. 2022, Trends Parasitol

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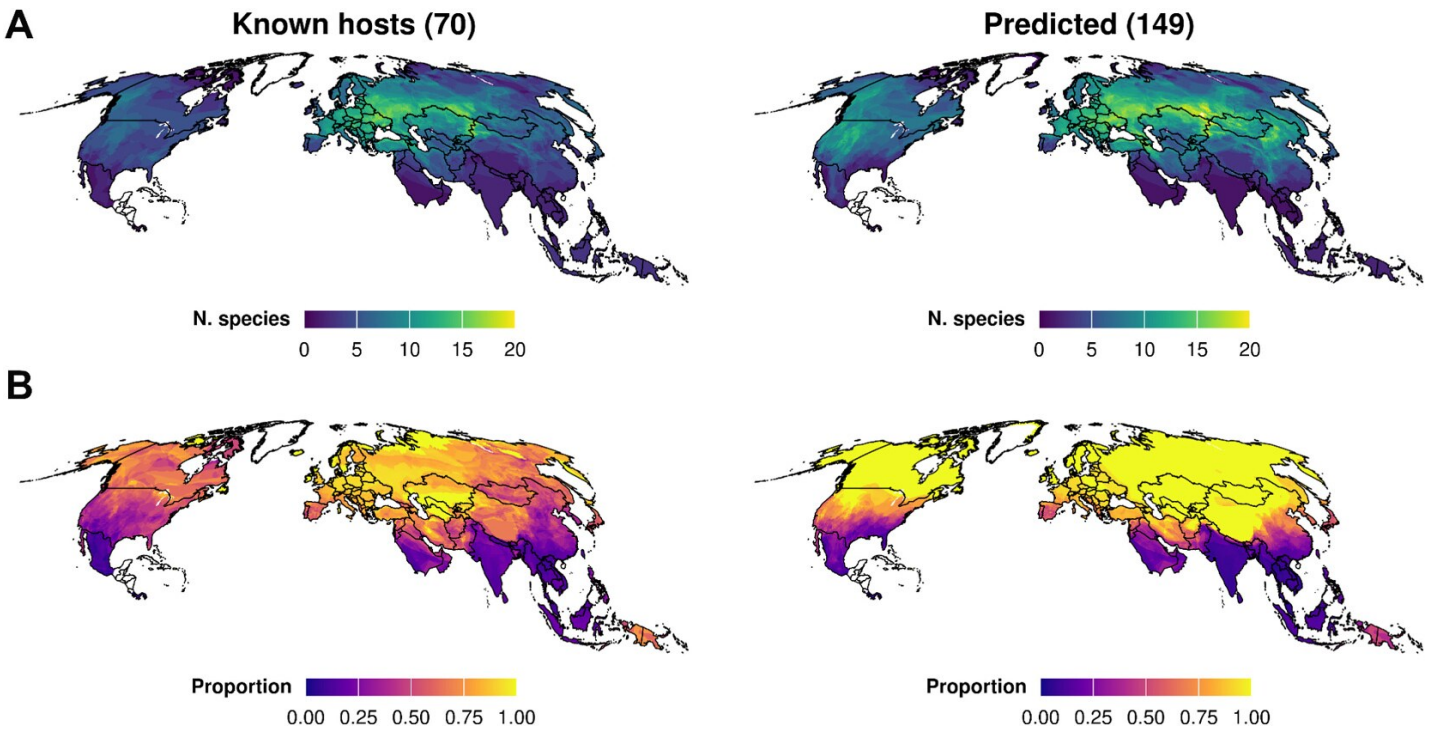
THE HOST MAP IS BIGGER THAN THE KNOWN MAP



Simoncini et al. 2025, Ecol Inform · code & data: zenodo.org/doi/10.5281/zenodo.13225482

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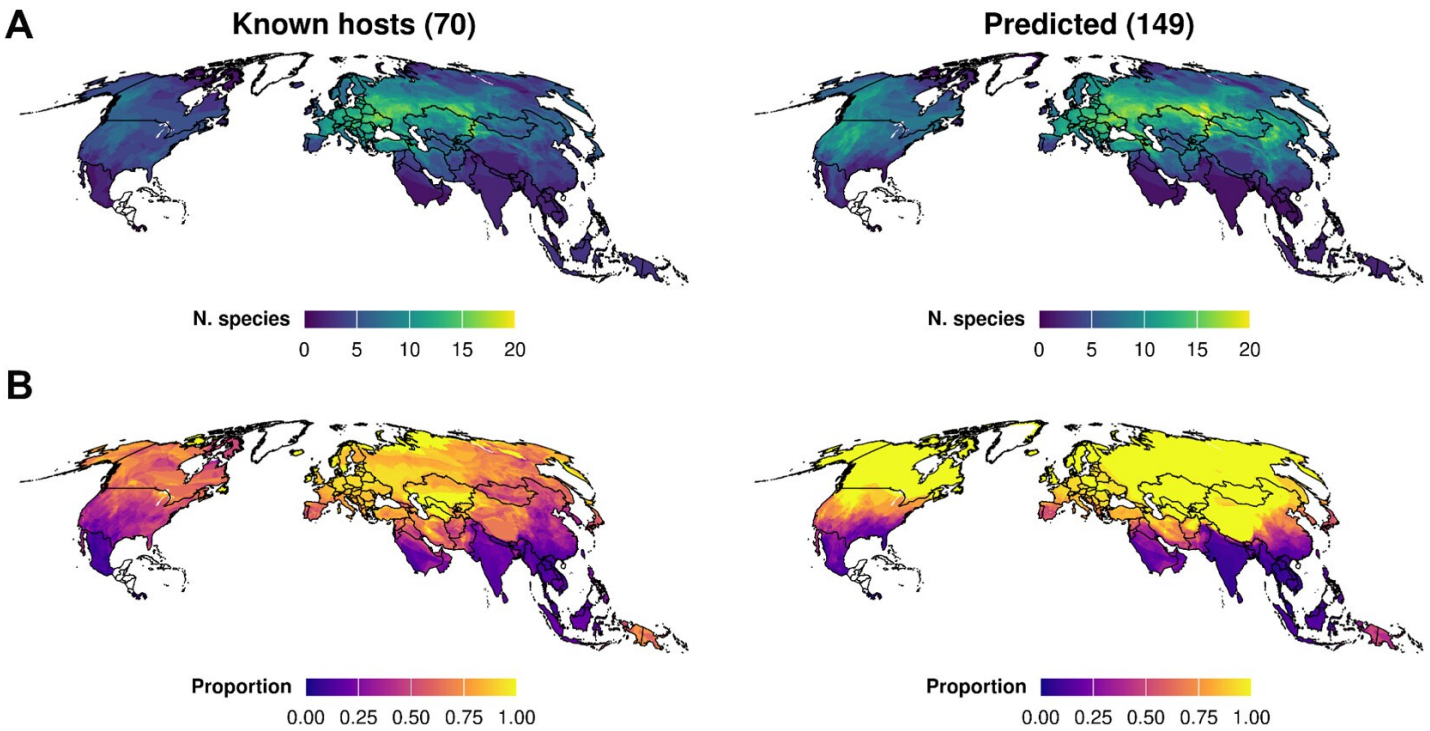
70

known rodent hosts

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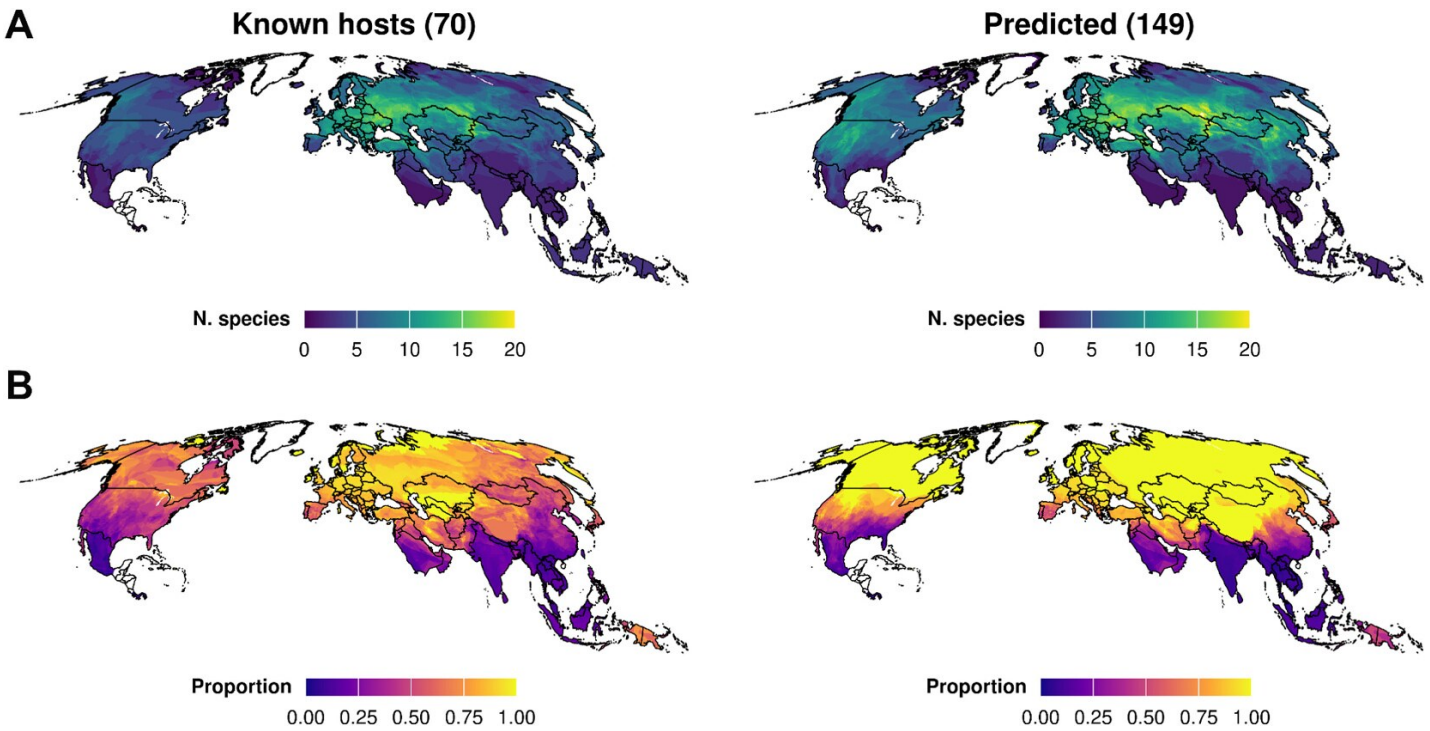


70 known rodent hosts → **149** predicted susceptible

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known rodent hosts — predicted susceptible

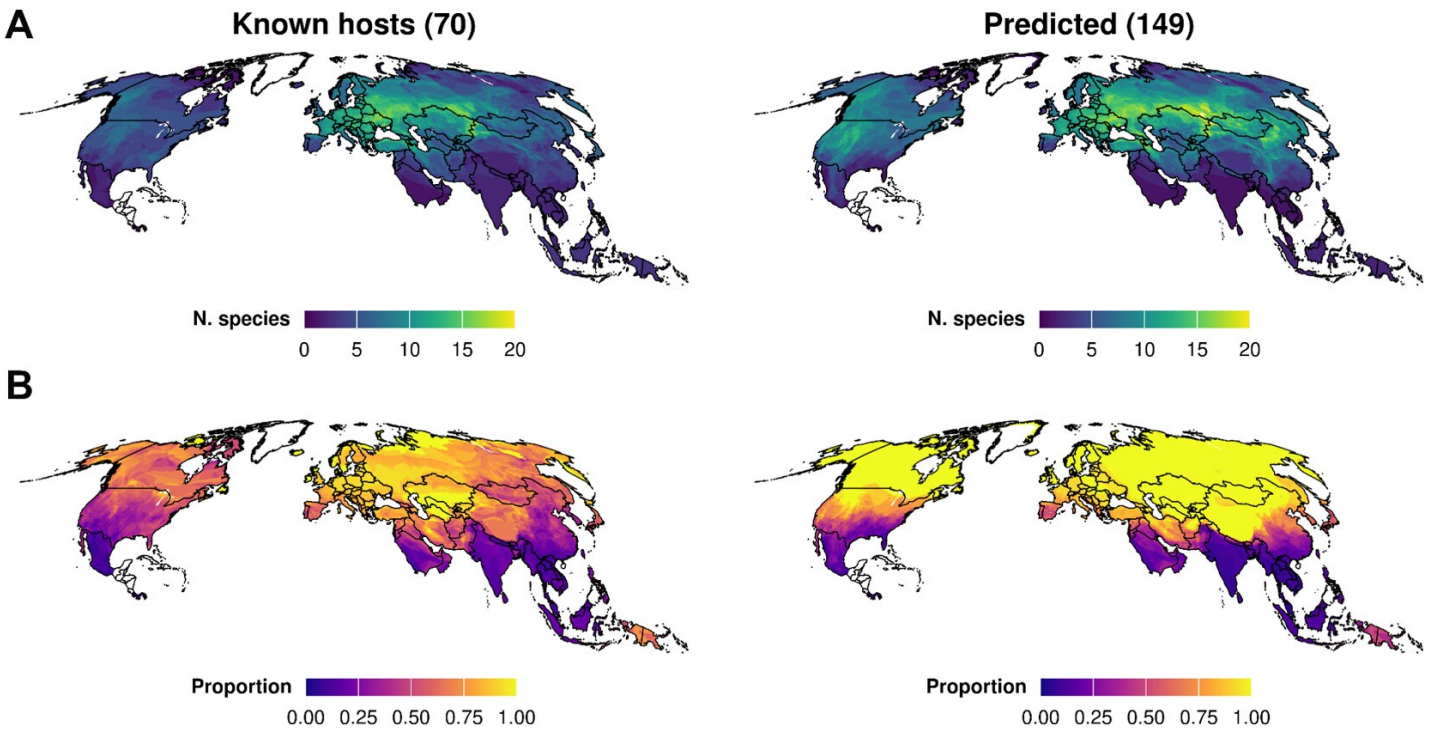
Richness of predicted hosts peaks in central-eastern Europe, western North America and central Asia

Best predictors: mean temperature across the species range and range size

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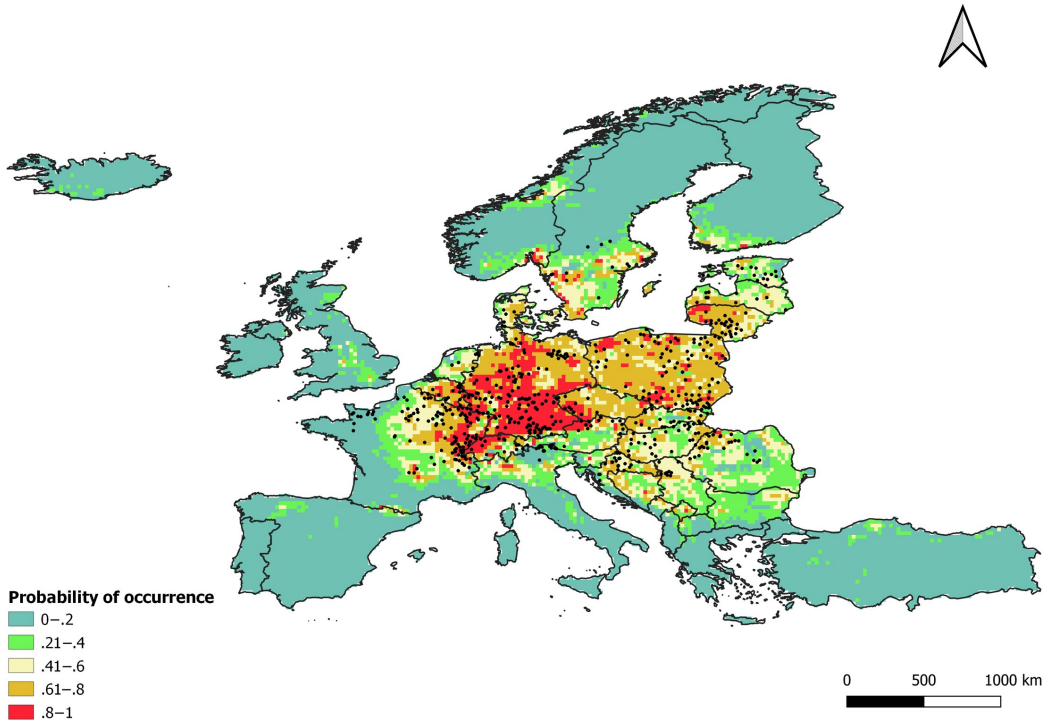
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UNREPORTED HOSTS = UNDERESTIMATED RISK

Simoncini et al. 2025, Ecol Inform · code & data: zenodo.org/doi/10.5281/zenodo.13225482

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DRIVER 3 · CLIMATE AND LAND USE SET THE STAGE

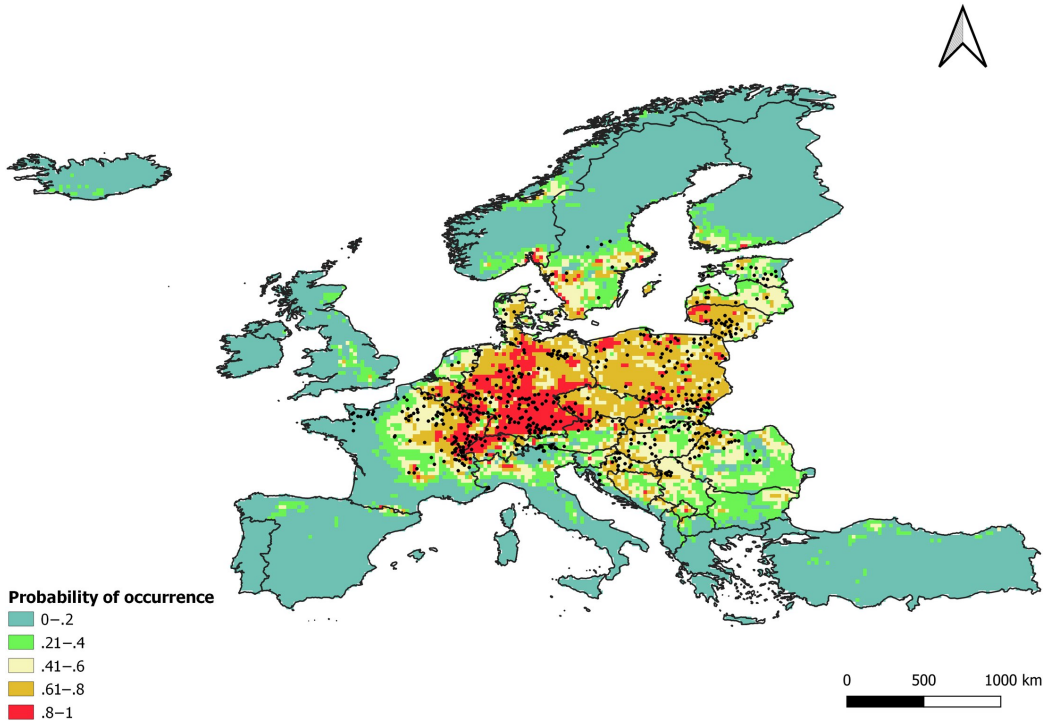


Current probability of occurrence

Cenni et al. 2023, Glob Change Biol – Maxent, 7 hypothesis-based predictor sets, SSP1-2.6 / SSP3-4.5 / SSP5-8.5

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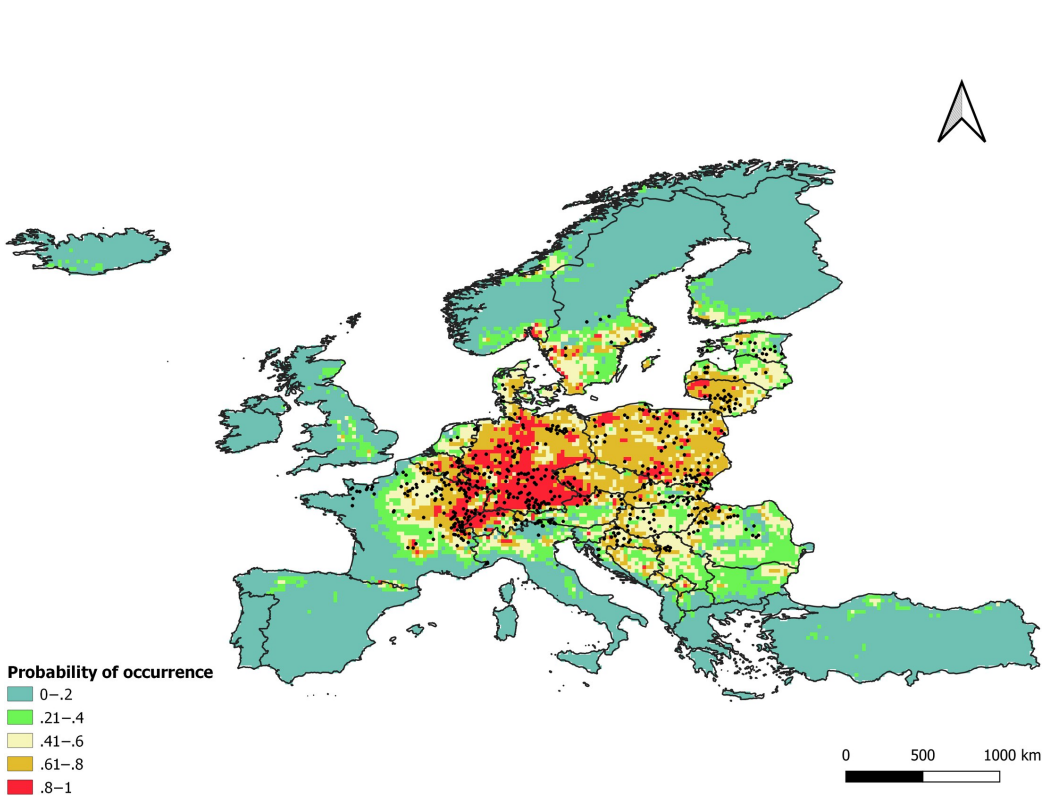
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59% of model contribution from the mean temperature of the coldest quarter

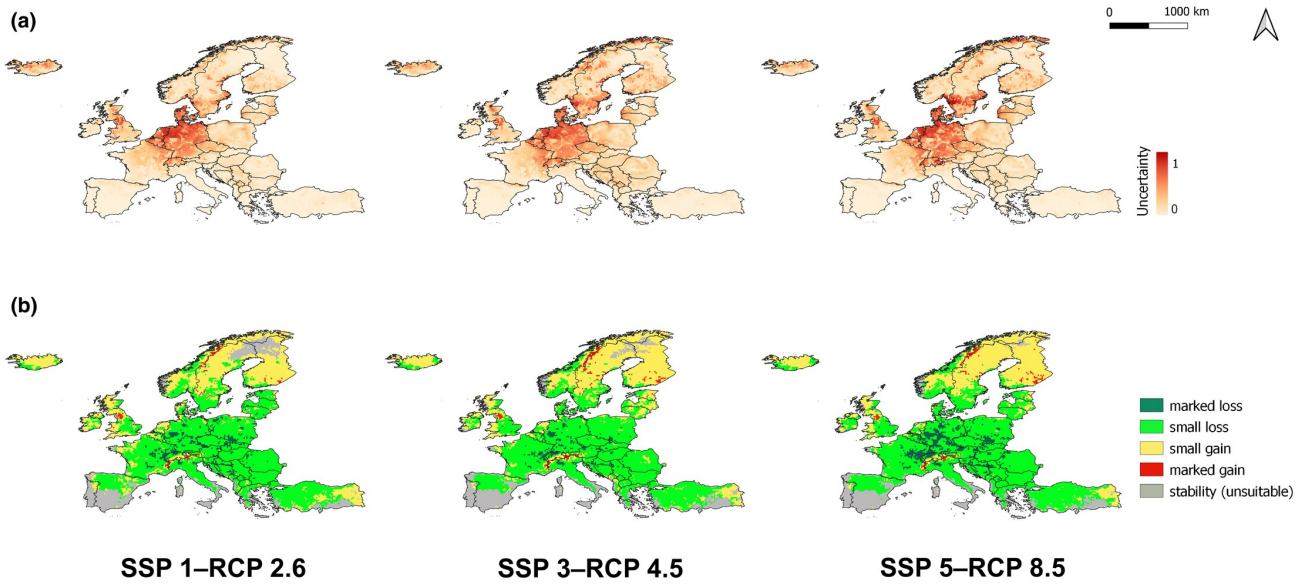
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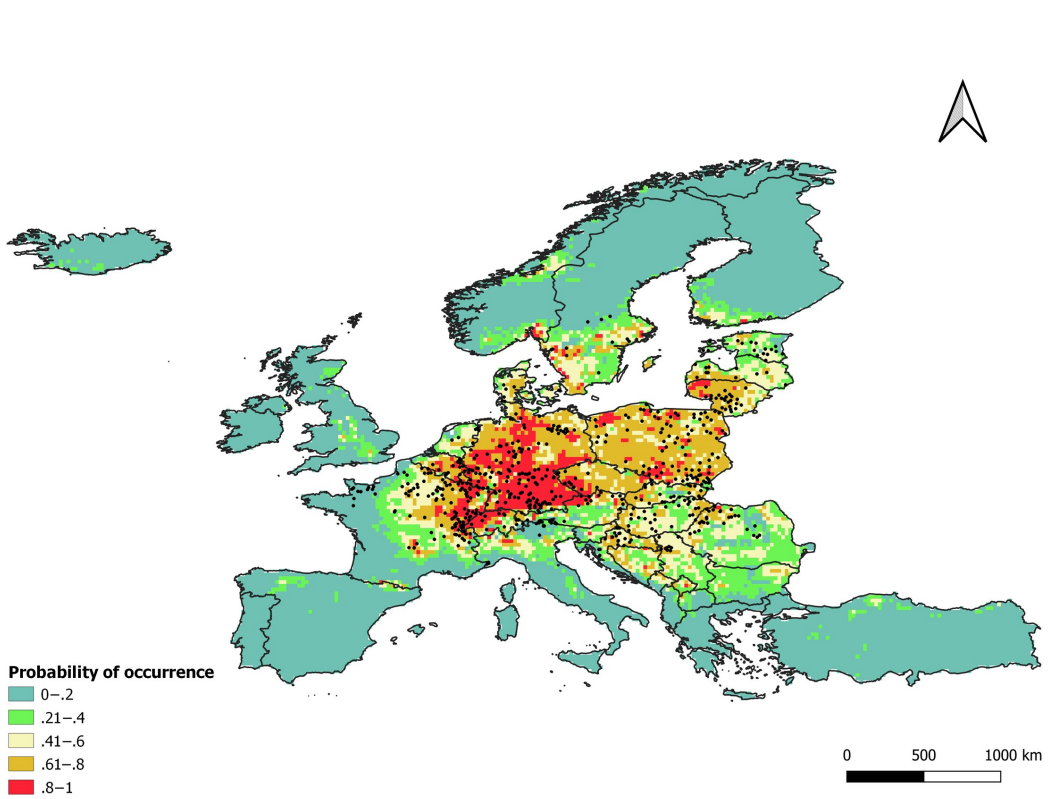


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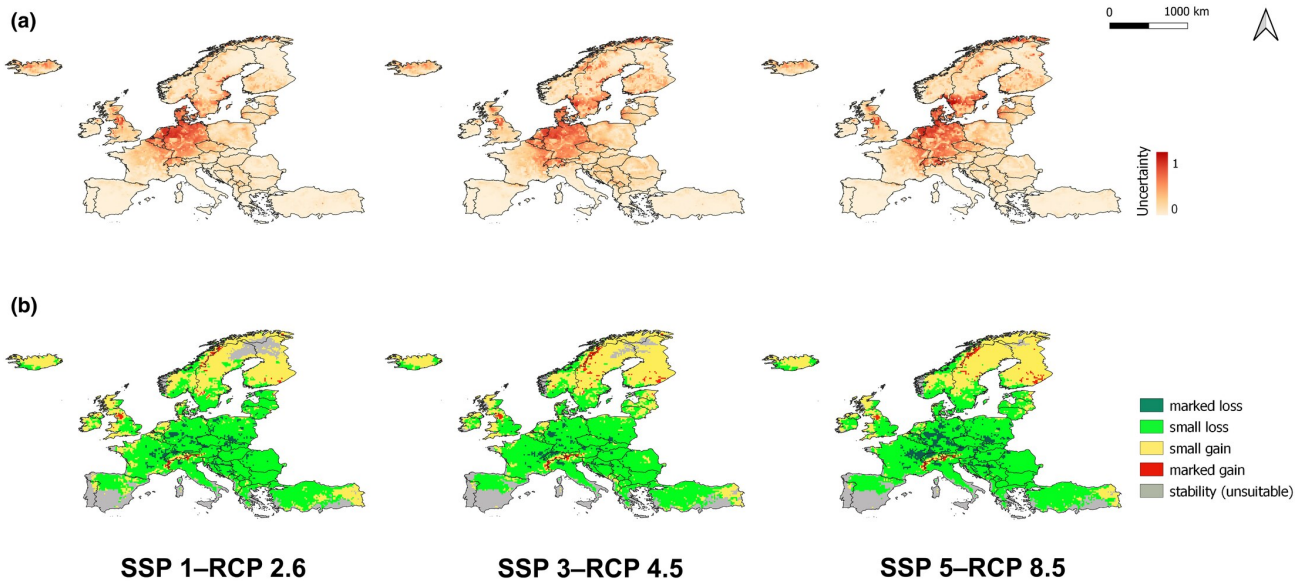
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DRIVER 3 · CLIMATE AND LAND USE SET THE STAGE



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GAINS NORTHWARD AND ACROSS THE ALPS · LOSSES IN CENTRAL EUROPE

Cenni et al. 2023, Glob Change Biol – Maxent, 7 hypothesis-based predictor sets, SSP1-2.6 / SSP3-4.5 / SSP5-8.5

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BUT LOCALLY, MICROCLIMATE CAN BEAT MACROCLIMATE

SW Hungary · response: apparent prevalence at necropsy (small intestine), 197 red foxes + 194 golden jackals, 2021–2022

Moloi et al. 2023, Sci Rep — OLS, GWR and multiscale GWR; standardised coefficients

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GLOBAL EFFECT

WETLANDS

$$\beta = +0.39$$

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PRECIPITATION SEASONALITY

$\beta = -0.21$

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WET PATCHES CAN CARRY THE CYCLE INTO WARM REGIONS

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TAKE-HOME

FROM PATTERN TO PROCESS

TAKE-HOME

FROM PATTERN TO PROCESS

Climate and land use set the stage

TAKE-HOME

FROM PATTERN TO PROCESS

- Climate and land use set the stage
- Intermediate hosts draw the borders

TAKE-HOME

FROM PATTERN TO PROCESS

- Climate and land use set the stage
- Intermediate hosts draw the borders
- Definitive hosts – and people – move the parasite

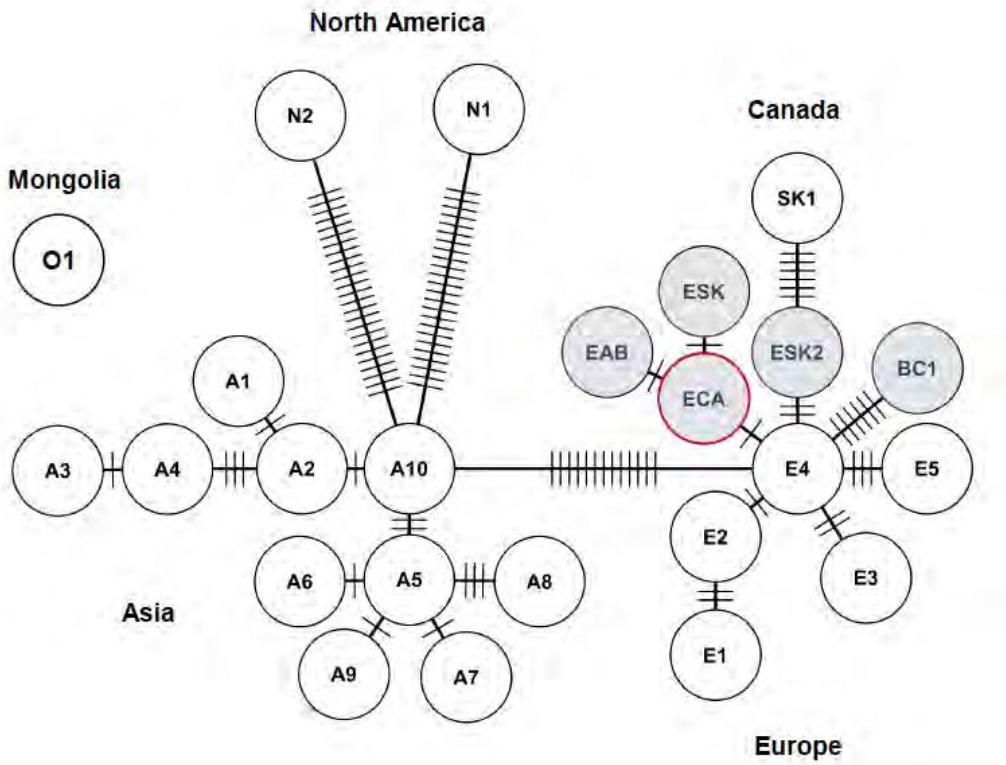
III

LESSONS FROM ACROSS THE ATLANTIC

North America as a natural experiment on processes



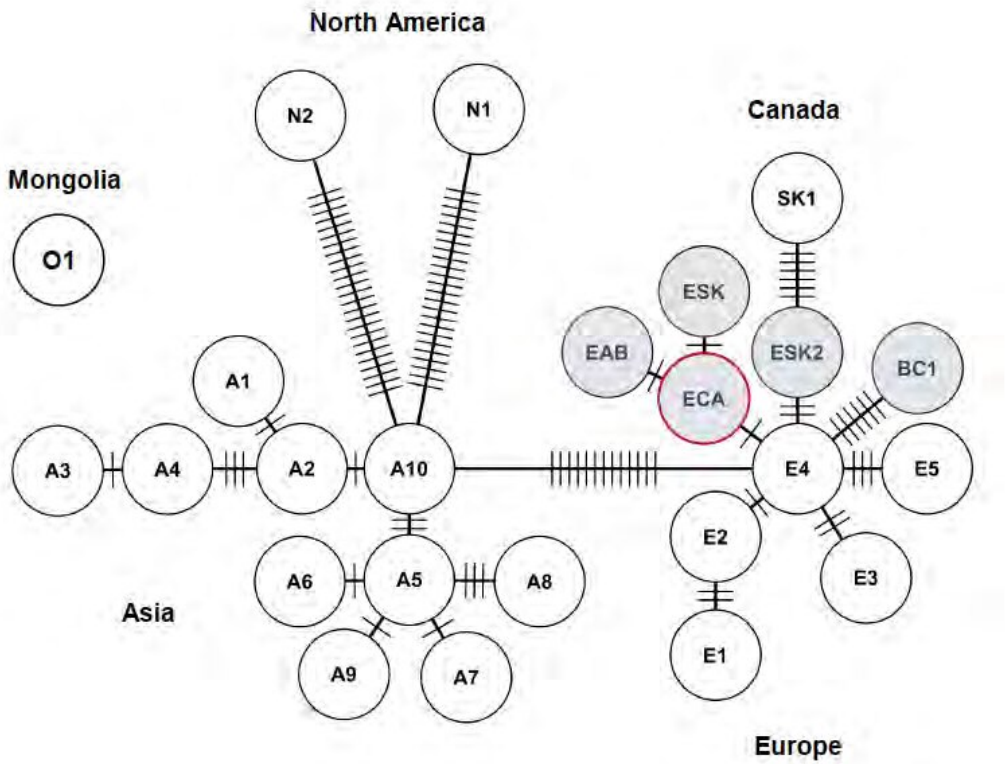
A EUROPEAN PARASITE IN WESTERN CANADA



Santa et al. 2023, Proc R Soc B · Gesy et al. 2014, IJP-PAW · Santa et al. 2021, Parasitology

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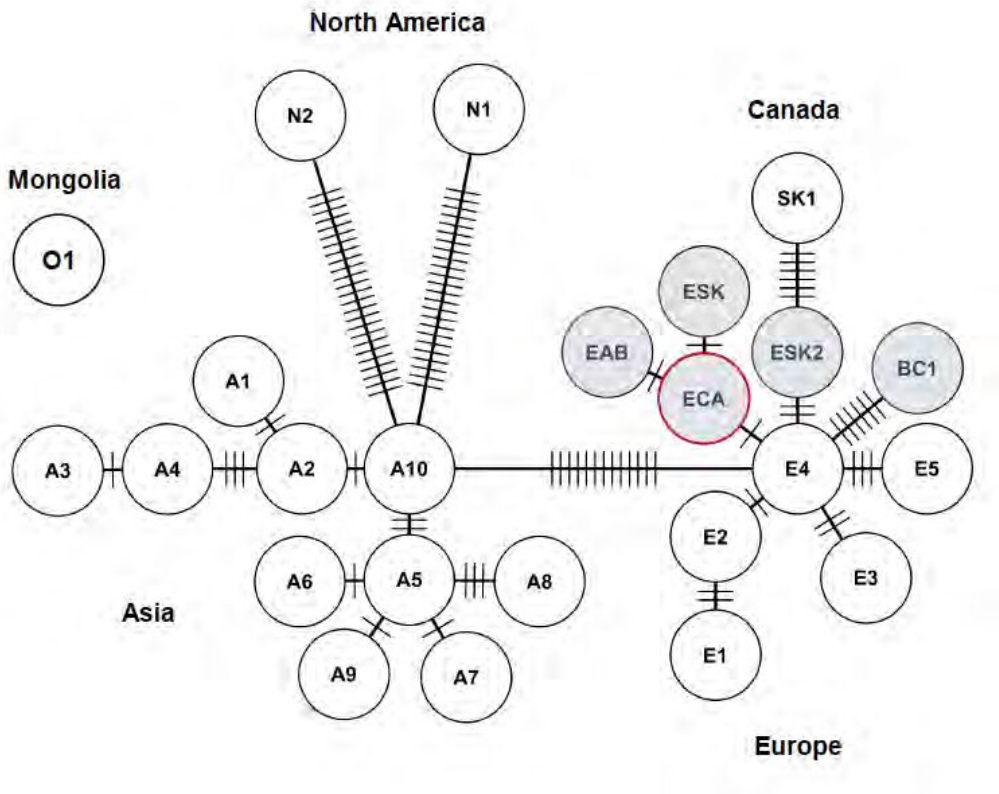
93/96 worms with European-like haplotypes

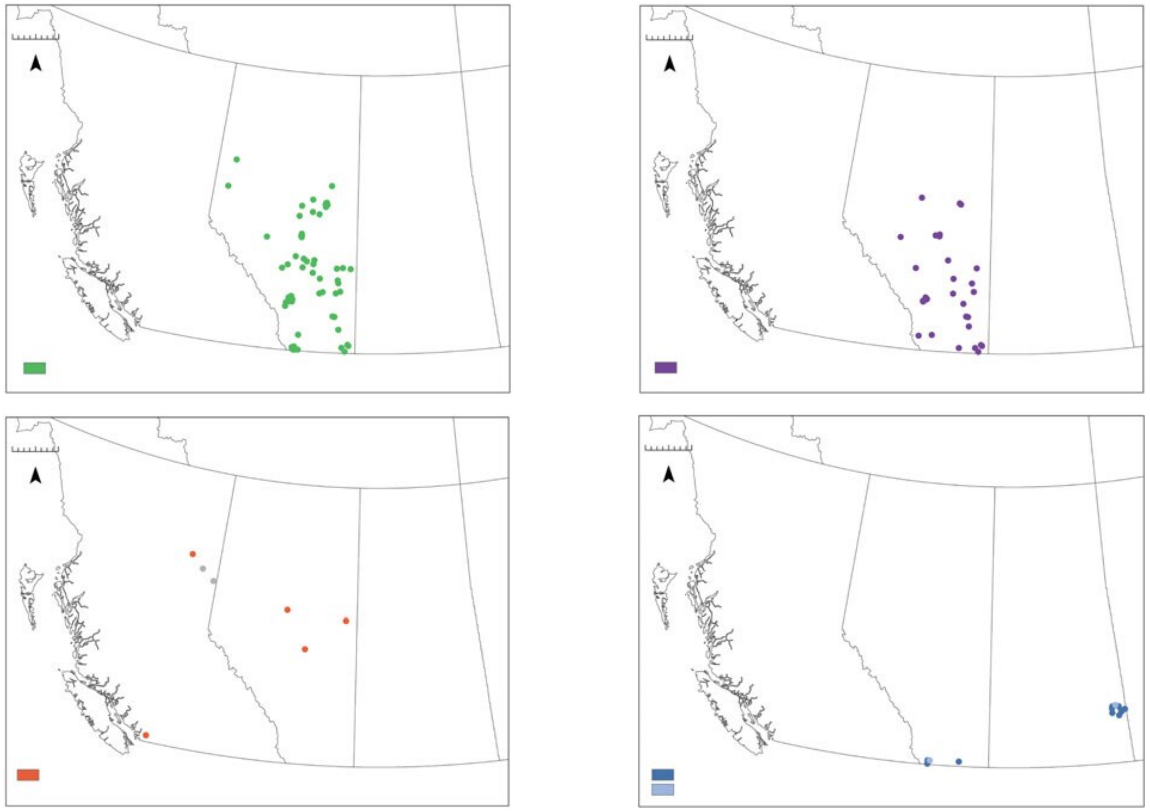
Santa et al. 2023, Proc R Soc B – cox1, nad2, cob; 13 foxes, 77 coyotes · network: same paper

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A EUROPEAN PARASITE IN WESTERN CANADA





EmsB profiles in western Canada: Santa et al. 2023, Proc R Soc B (Fig. 5)

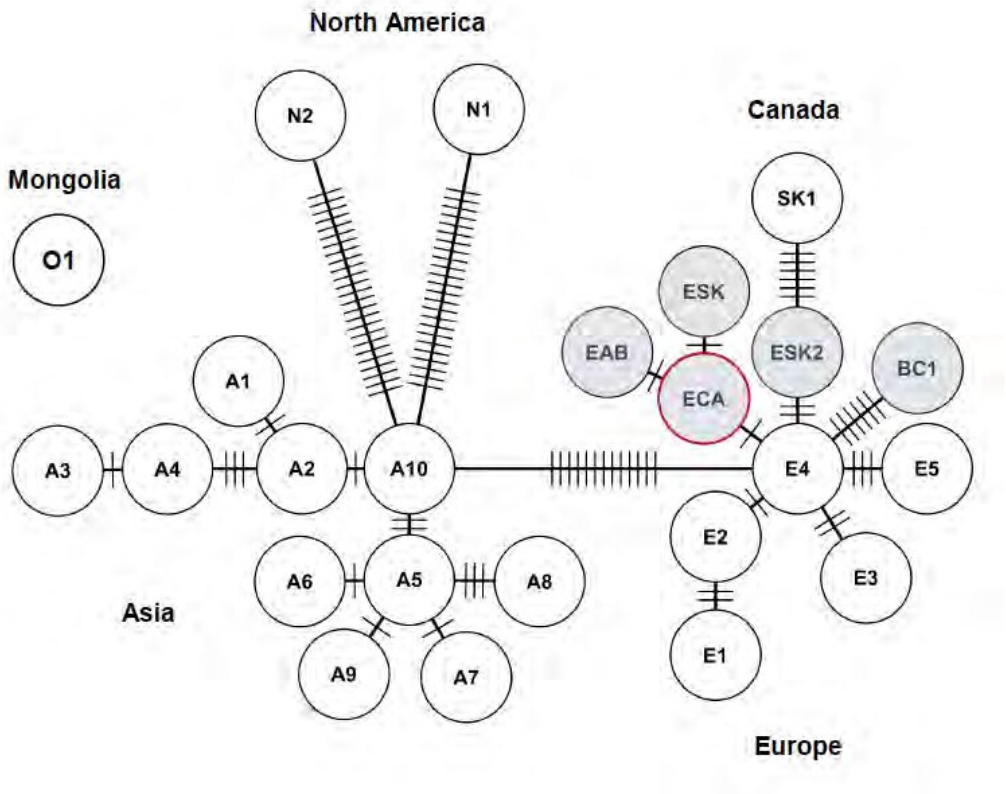
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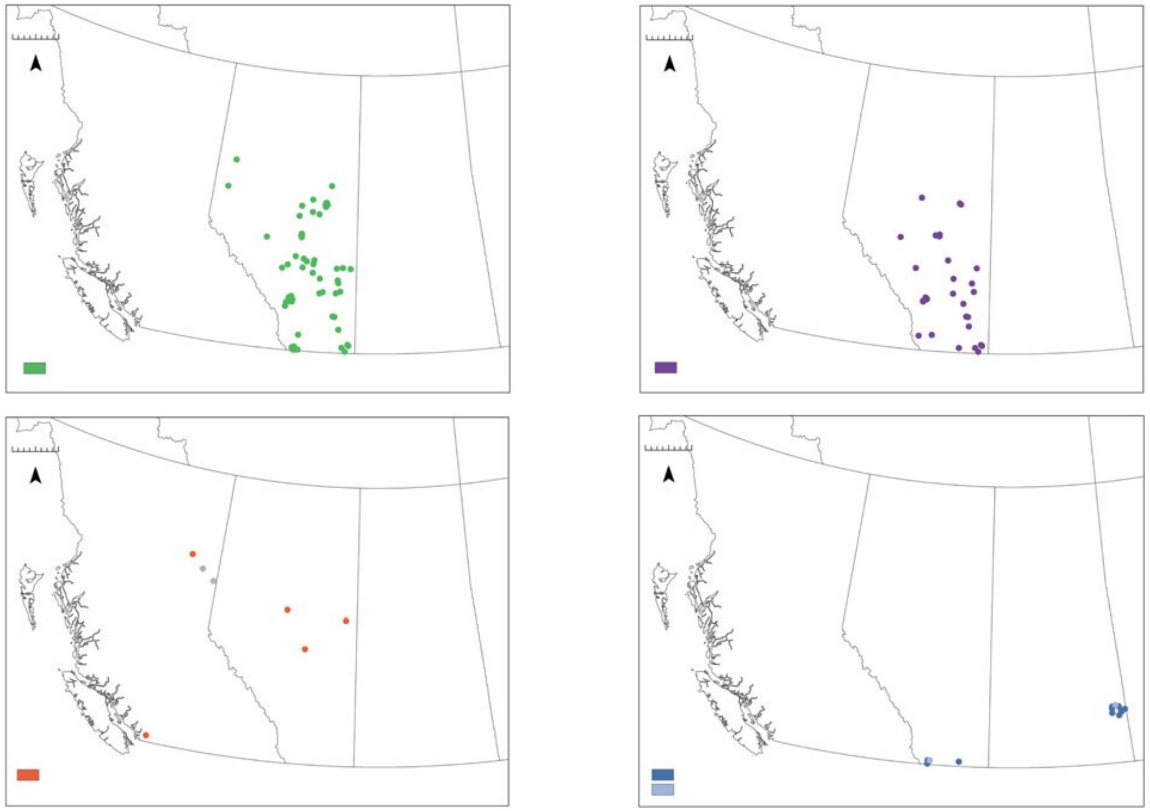
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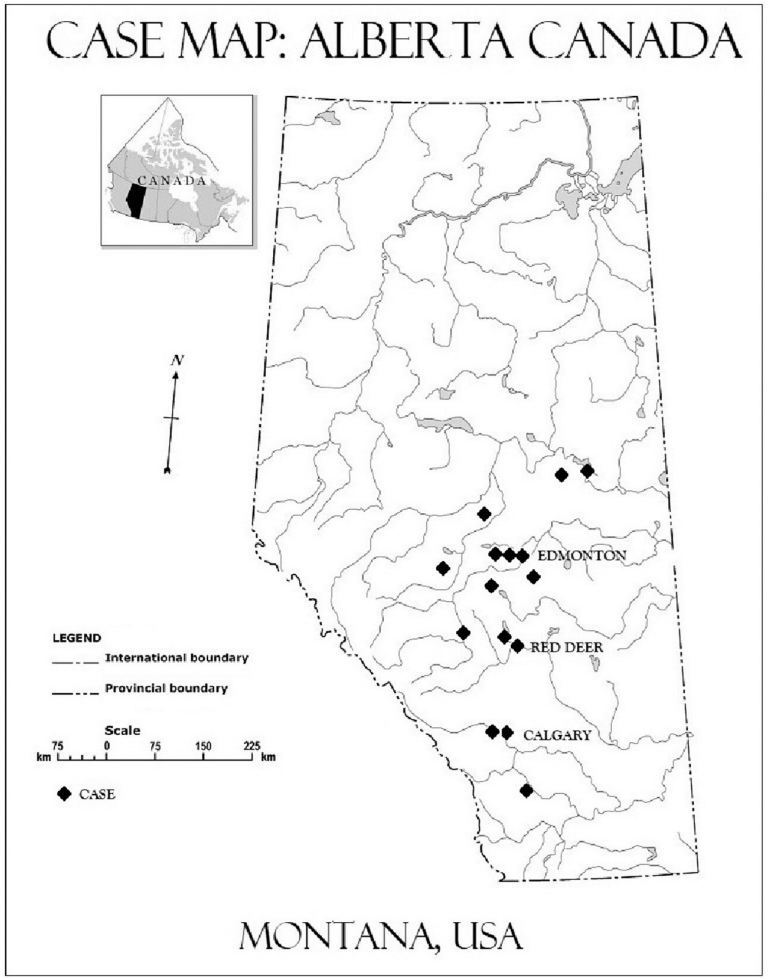
Santa et al. 2023, Proc R Soc B – cox1, nad2, cob; 13 foxes, 77 coyotes · network: same paper

LOW DIVERSITY + SPATIAL DISCONTINUITIES = RECENT INVASION, SEVERAL FOUNDERS

Santa et al. 2023, Proc R Soc B · Gesy et al. 2014, IJP-PAW · Santa et al. 2021, Parasitology

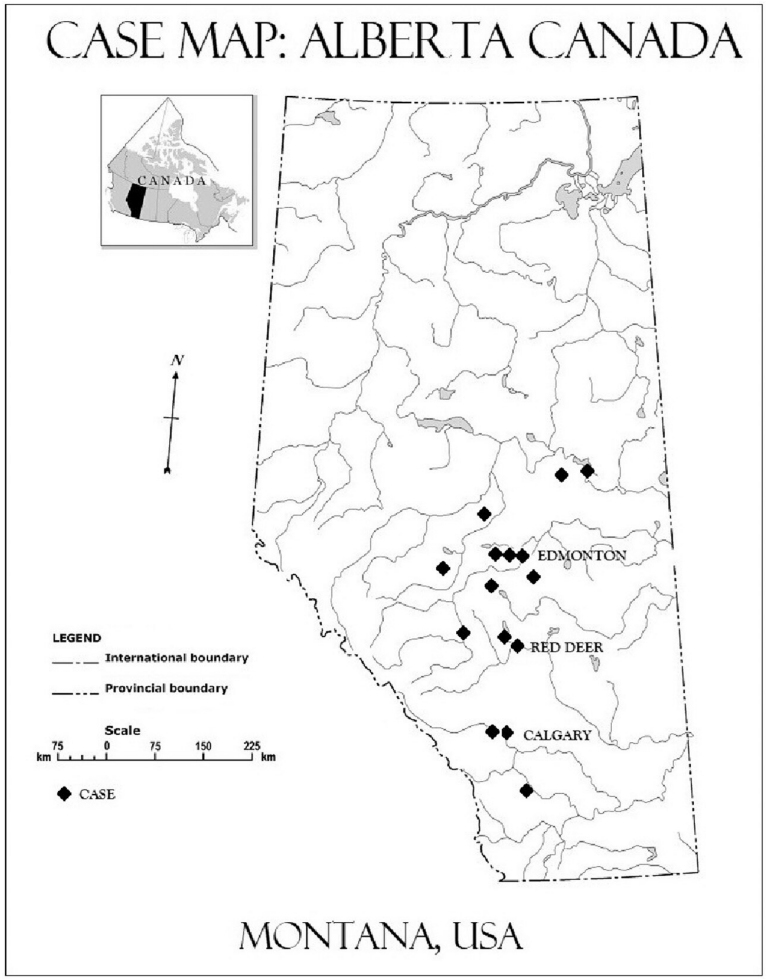
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FROM WILDLIFE TO PATIENTS: AN EMERGING DISEASE



Map of Alberta AE cases: Houston et al. 2021, Am J Trop Med Hyg

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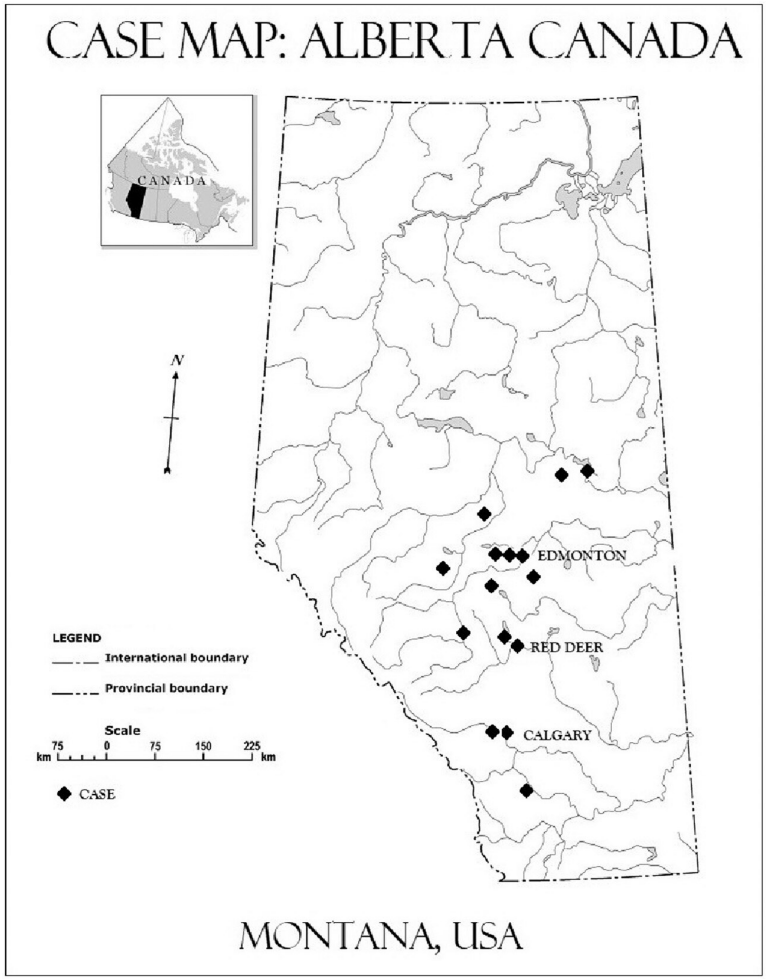
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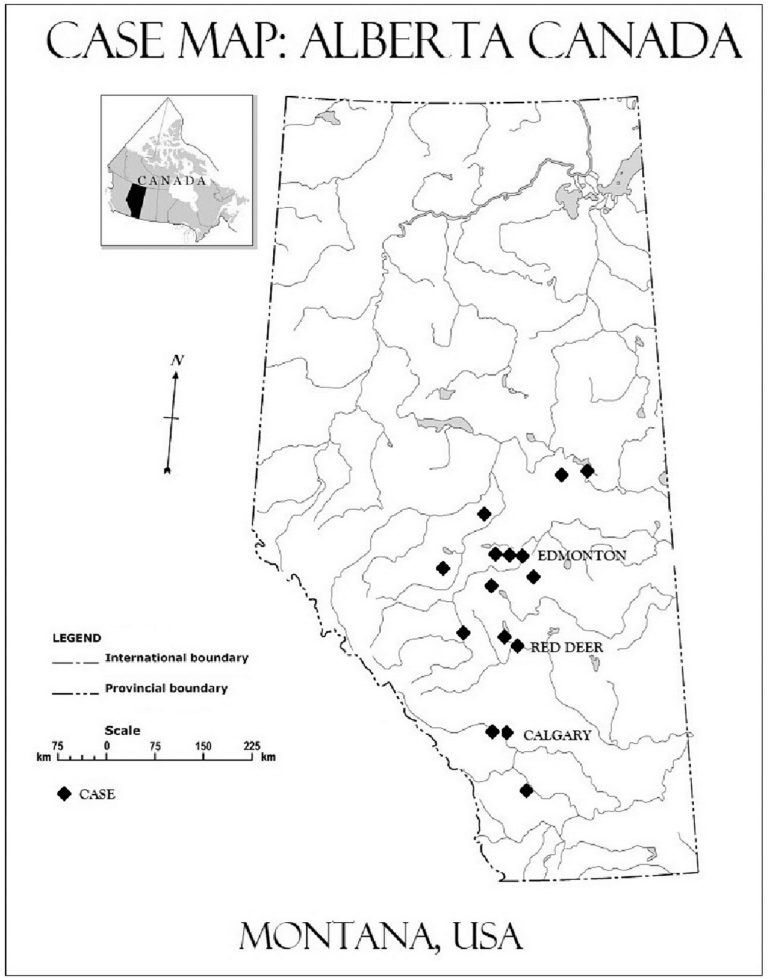
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7 AE patients in Alberta, 2013–2017 · incidence 0.059 per 100,000 population per year · 6 with European-type strain

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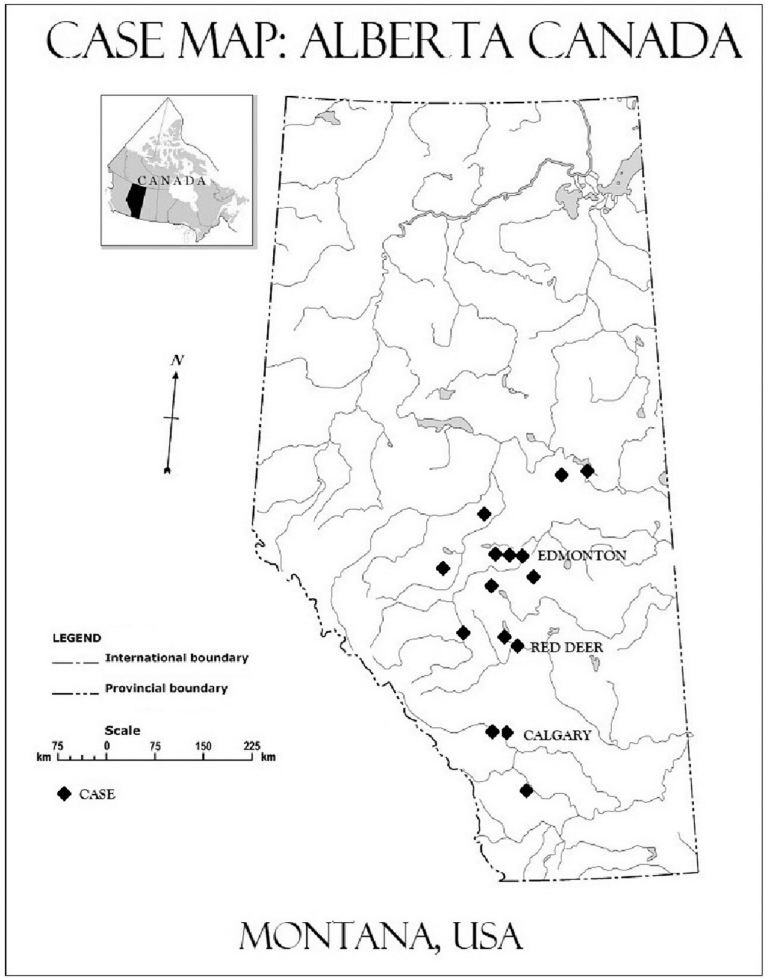
Massolo et al. 2019, N Engl J Med

17 AE cases acquired in Alberta, 2013–2020 · 6 immunocompromised · 14 had kept dogs

Houston et al. 2021, Am J Trop Med Hyg

A Massolo, Dept. Biology, Univ. Pisa | alessandro.massolo@unipi.it

FROM WILDLIFE TO PATIENTS: AN EMERGING DISEASE



Map of Alberta AE cases: Houston et al. 2021, Am J Trop Med Hyg

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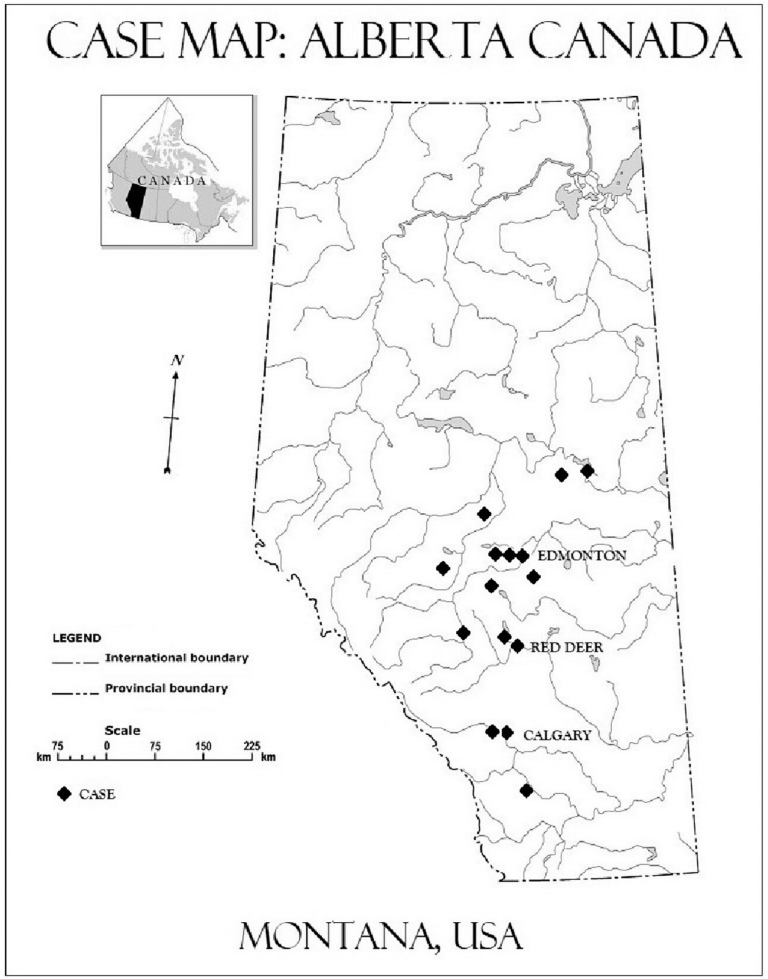
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42 PCR-confirmed AE cases in Alberta, 2013–2025

K. Kowalewska-Grochowska, pers. comm., Sept 2025

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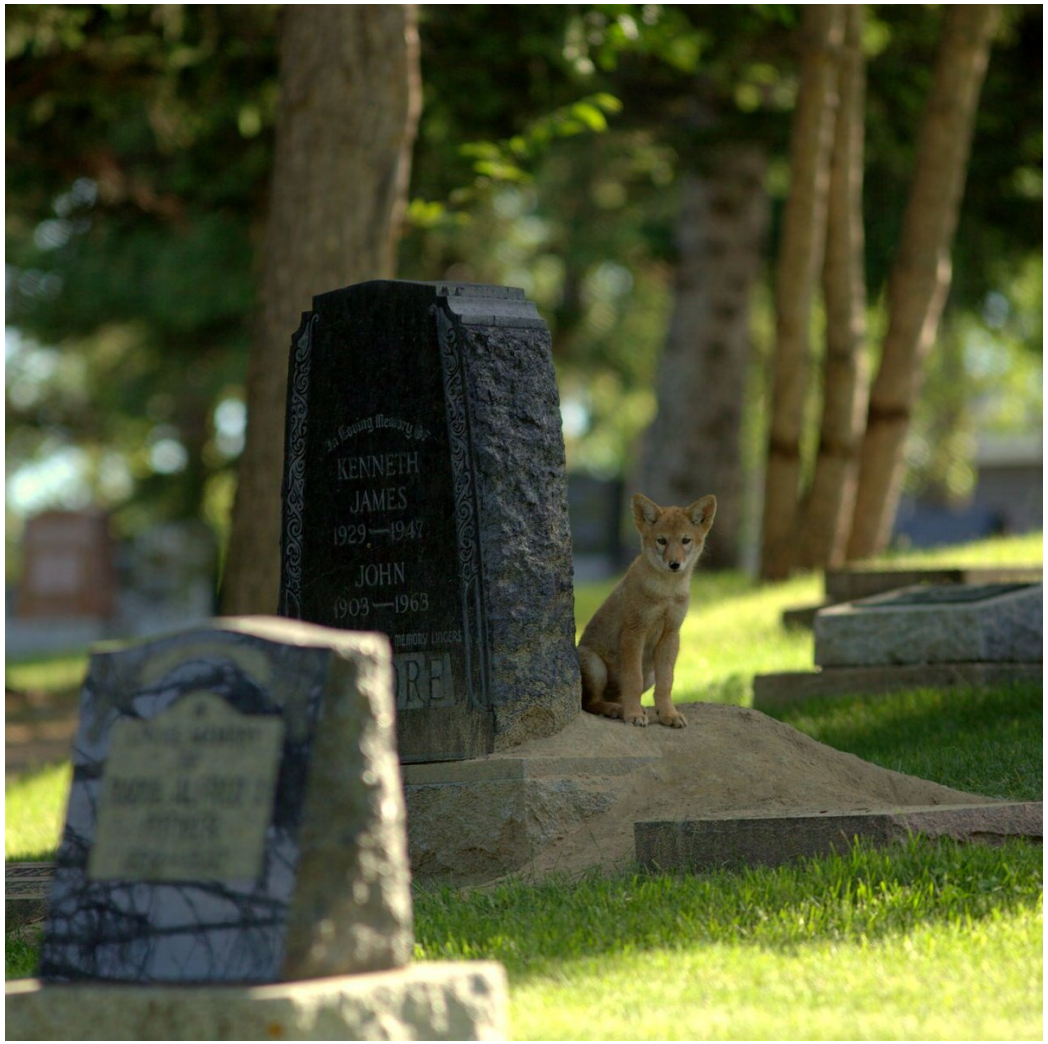
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AN INTRODUCED, VIRULENT STRAIN CAN CHANGE THE RISK IN A DECADE

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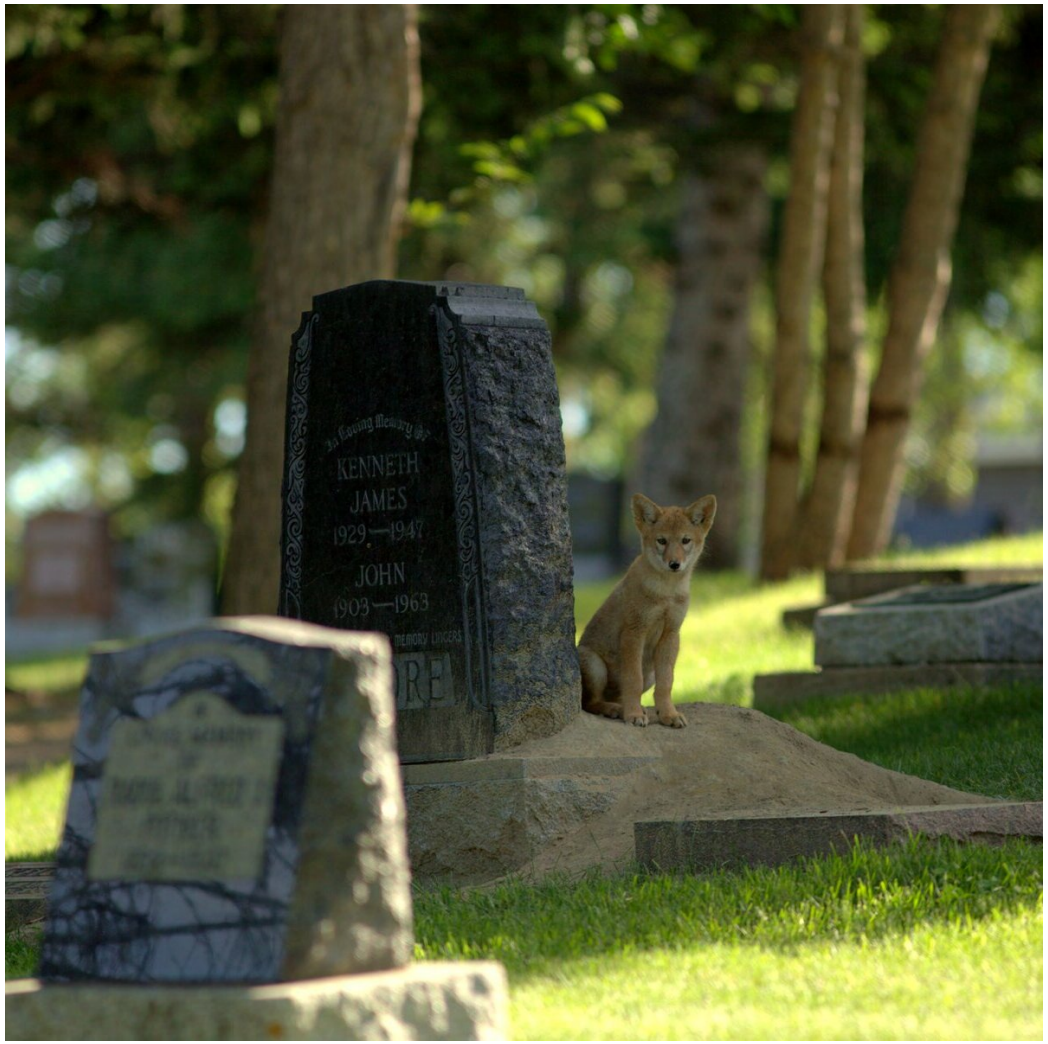
CITY SCALE: SAME CITY, TEN-FOLD DIFFERENCES



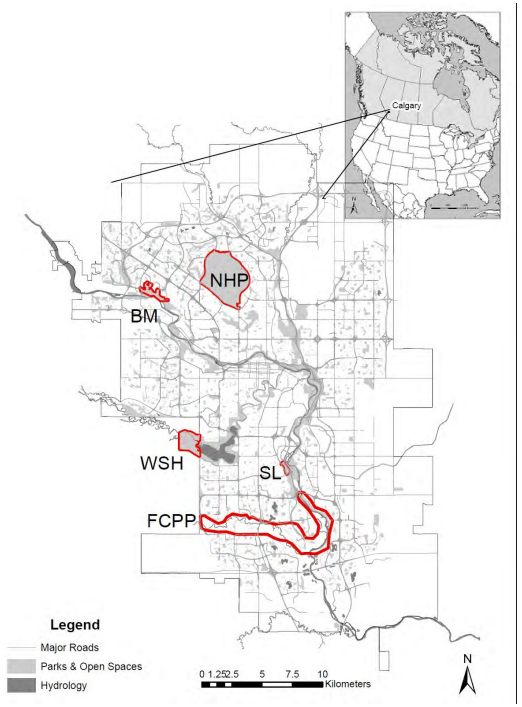
First detection in urban coyotes: Catalano et al. 2012, Emerg Infect Dis

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APPARENT PREVALENCE · COYOTE FAECES

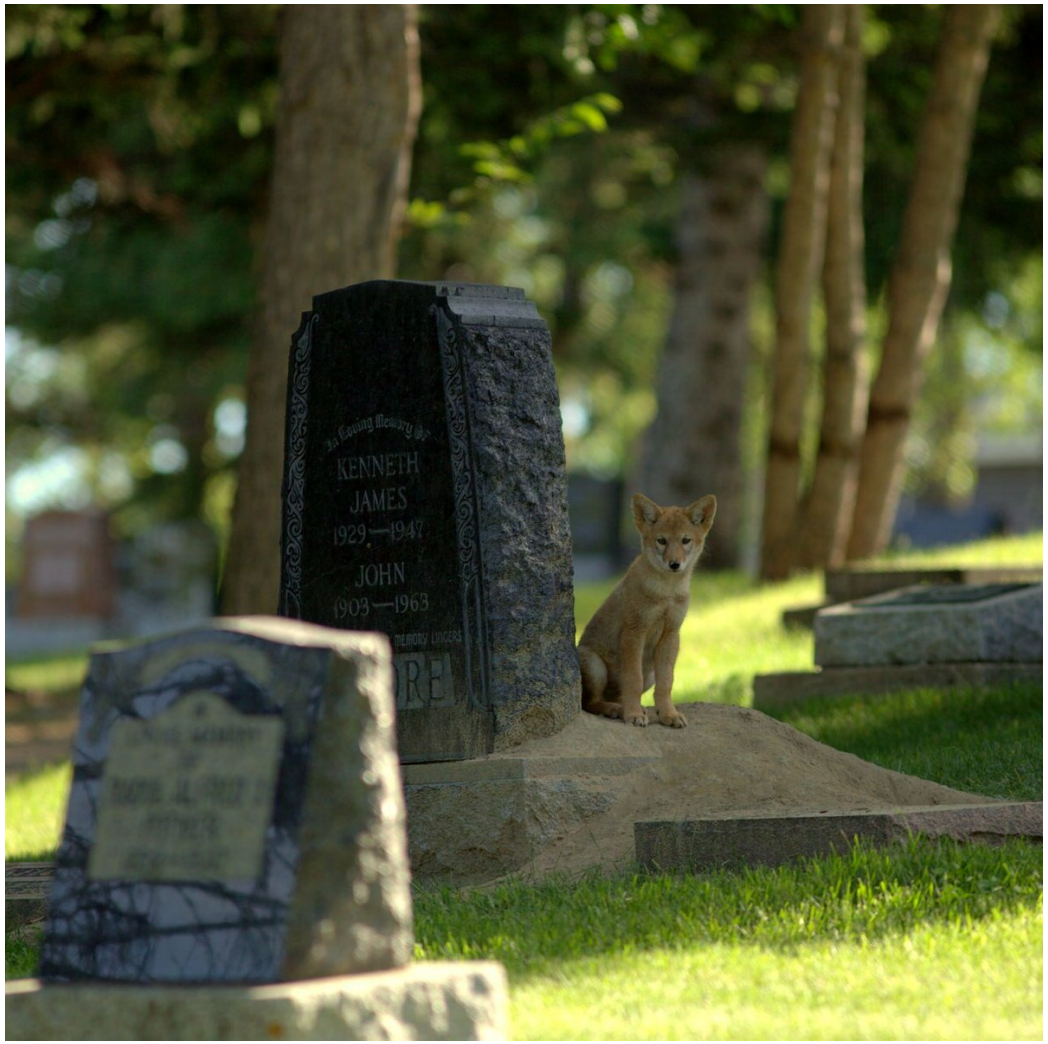
0.25

overall

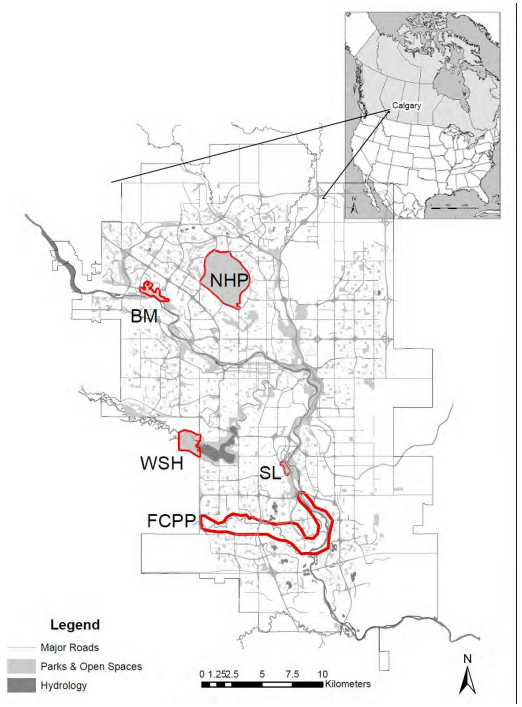
Liccioli et al. 2014, Int J Parasitol · Liccioli et al. 2015, J Appl Ecol – 5 city parks, 2012–2013

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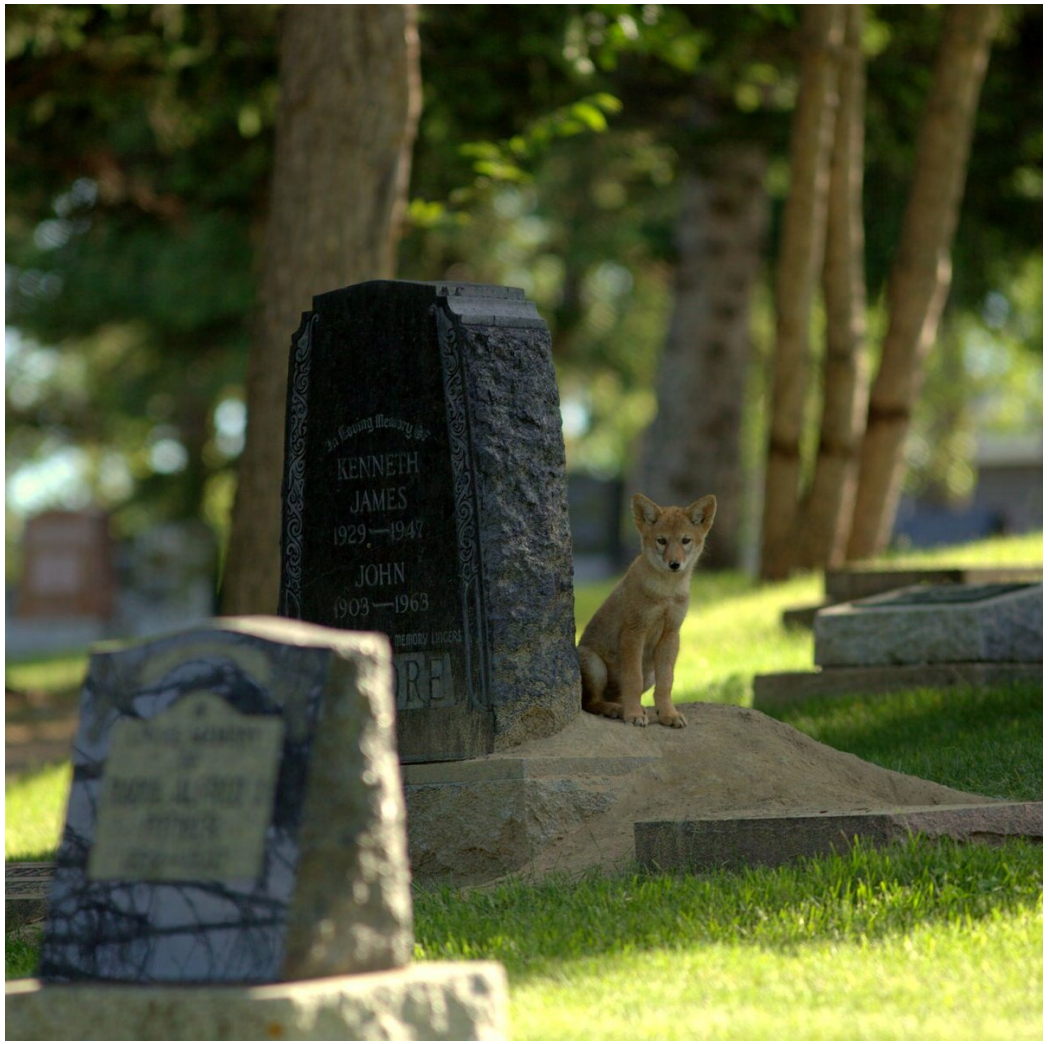
0.05–0.62

across city parks

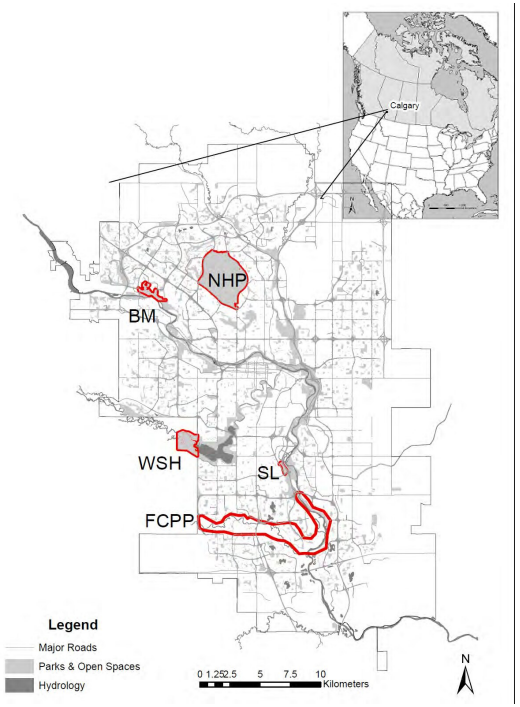
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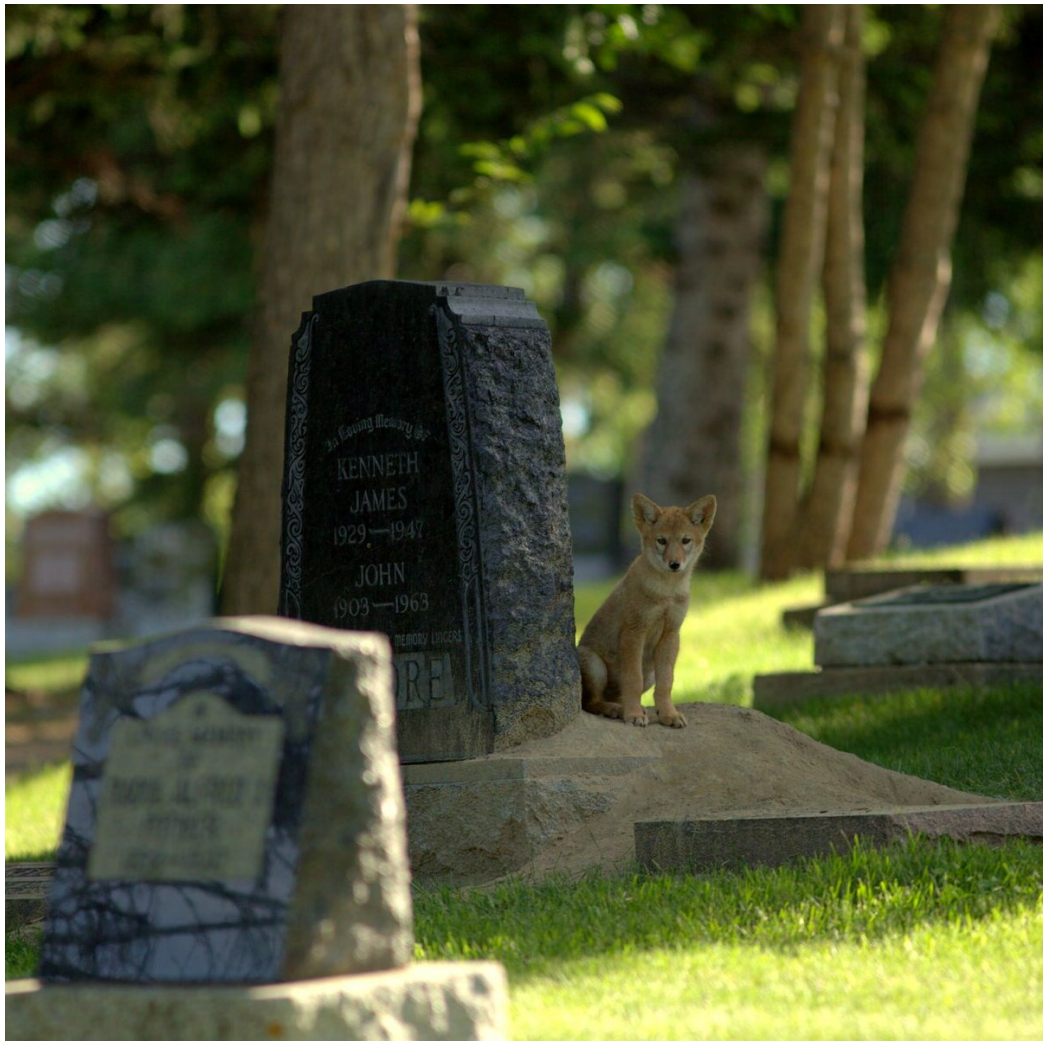
0.11–0.44

across seasons – winter peaks

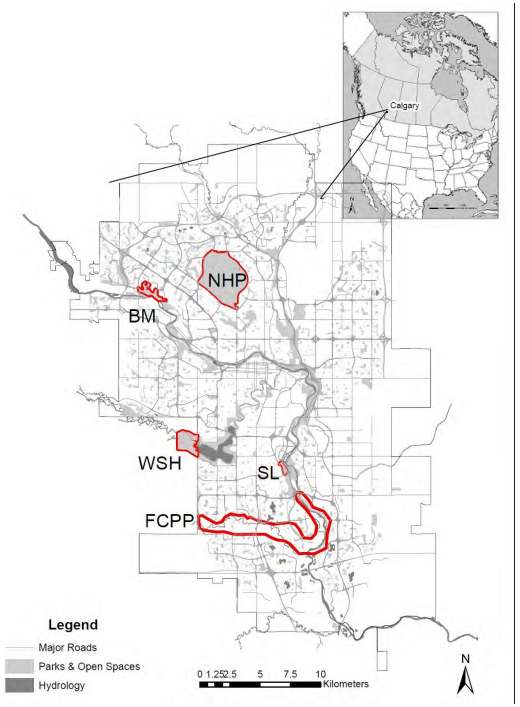
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HETEROGENEITY IS THE SIGNAL, NOT THE NOISE

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WHAT THE COYOTE EATS DECIDES WHERE THE PARASITE IS





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WHAT THE COYOTE EATS DECIDES WHERE THE PARASITE IS





Meadow vole & southern red-backed vole eaten more than their availability (251 faeces vs 971 trapped small mammals); encounter rate highest in winter

Liccioli et al. 2015, PLoS ONE 10

Southern red-backed vole, new IH: Liccioli et al. 2013, Parasitol Int

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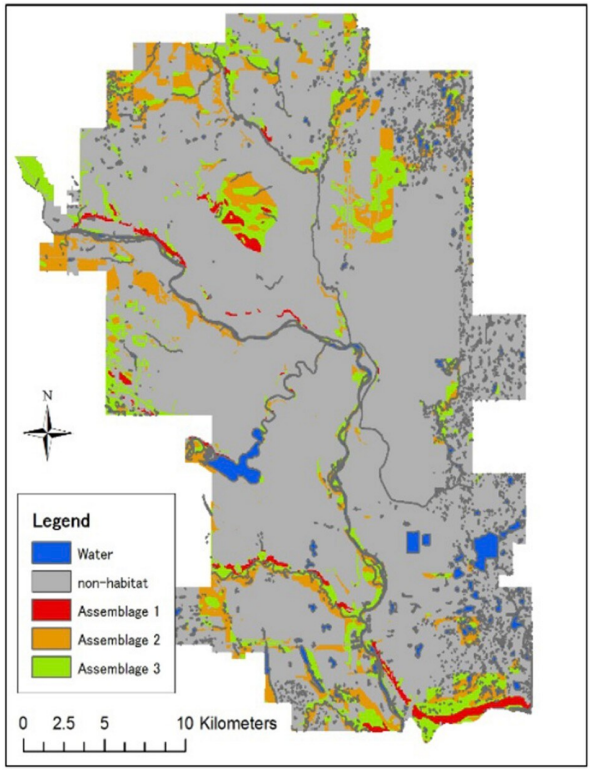
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Prey assemblages with more susceptible species → higher prevalence; total small-mammal abundance → no effect (dilution)

Mori et al. 2019, IJP-PAW



Map of small-mammal assemblages: Mori et al. 2019, IJP-PAW

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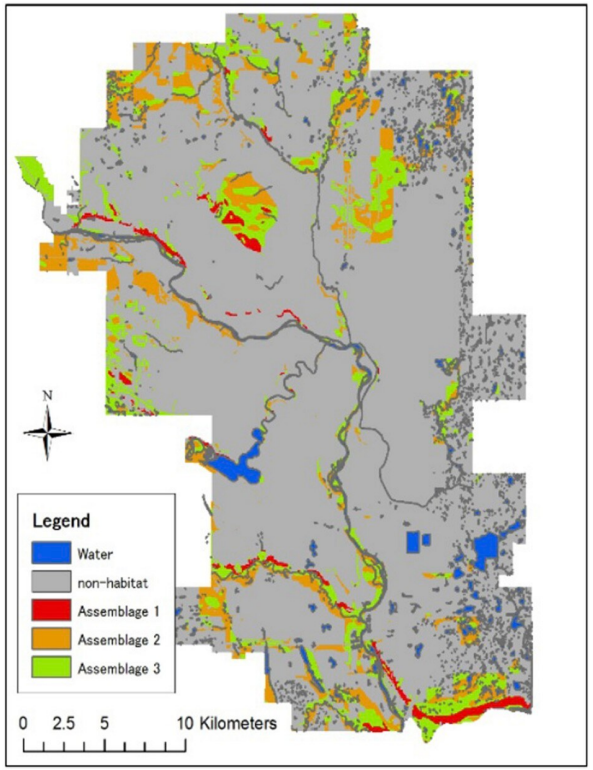
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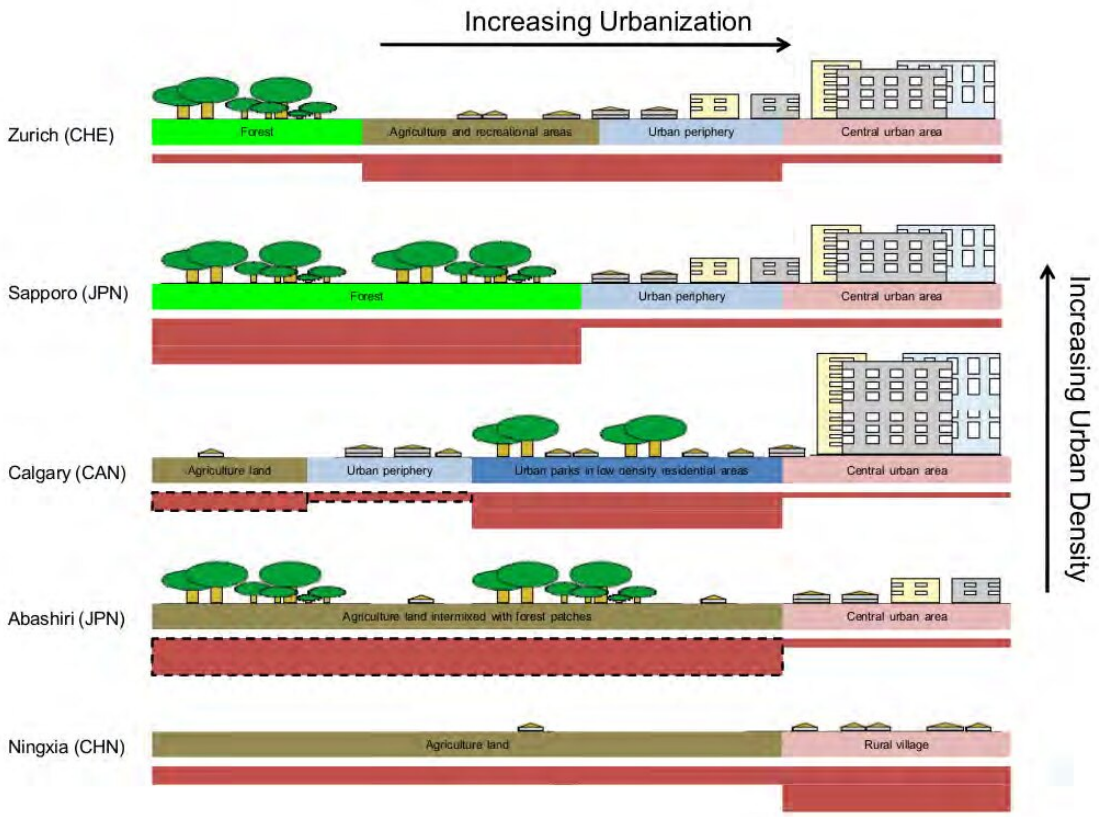


Map of small-mammal assemblages: Mori et al. 2019, IJP-PAW

COMMUNITY COMPOSITION, NOT PREY ABUNDANCE

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'URBAN' IS NOT ONE HABITAT: WHERE TRANSMISSION PEAKS

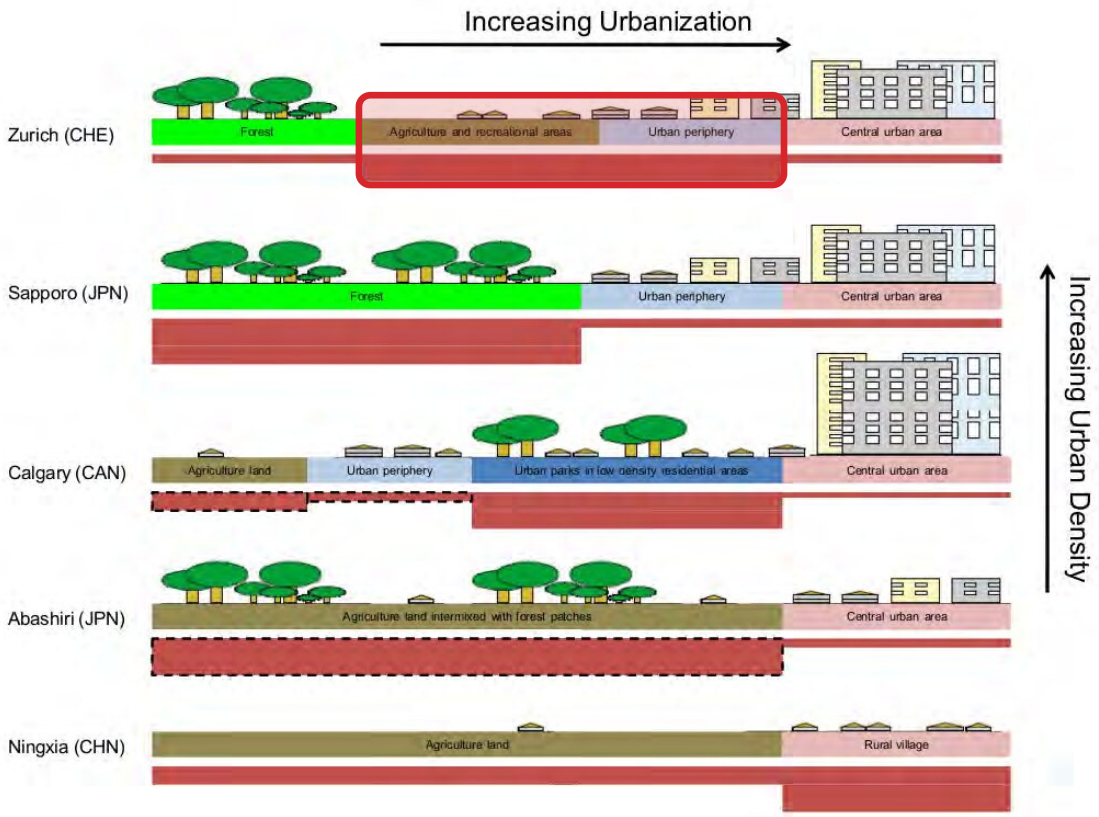


Red bars under each transect: relative transmission / prevalence in definitive hosts (thicker = higher; dashed = inferred from limited data)

Figure: Liccioli et al. 2015, Trends Parasitol · heterogeneity driven by IH distribution & habitat separation: Mori et al. 2023, Ecol Model

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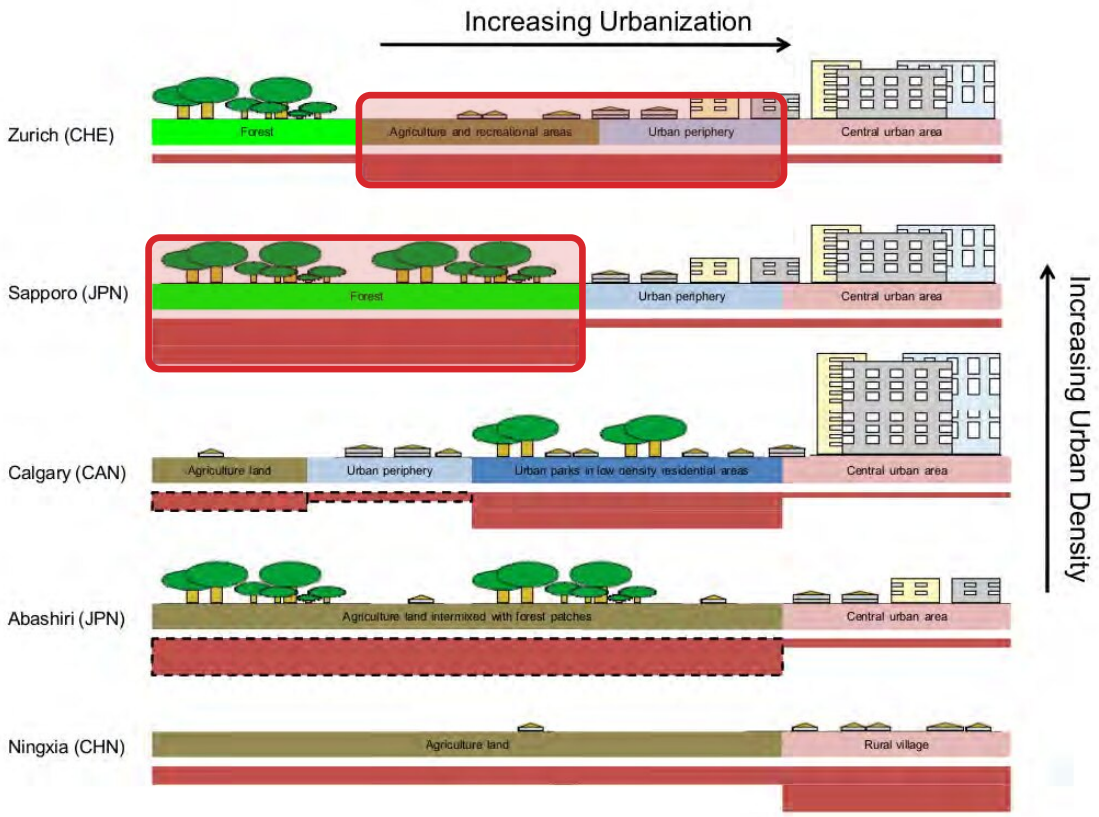
ZURICH agricultural & recreational areas and urban periphery

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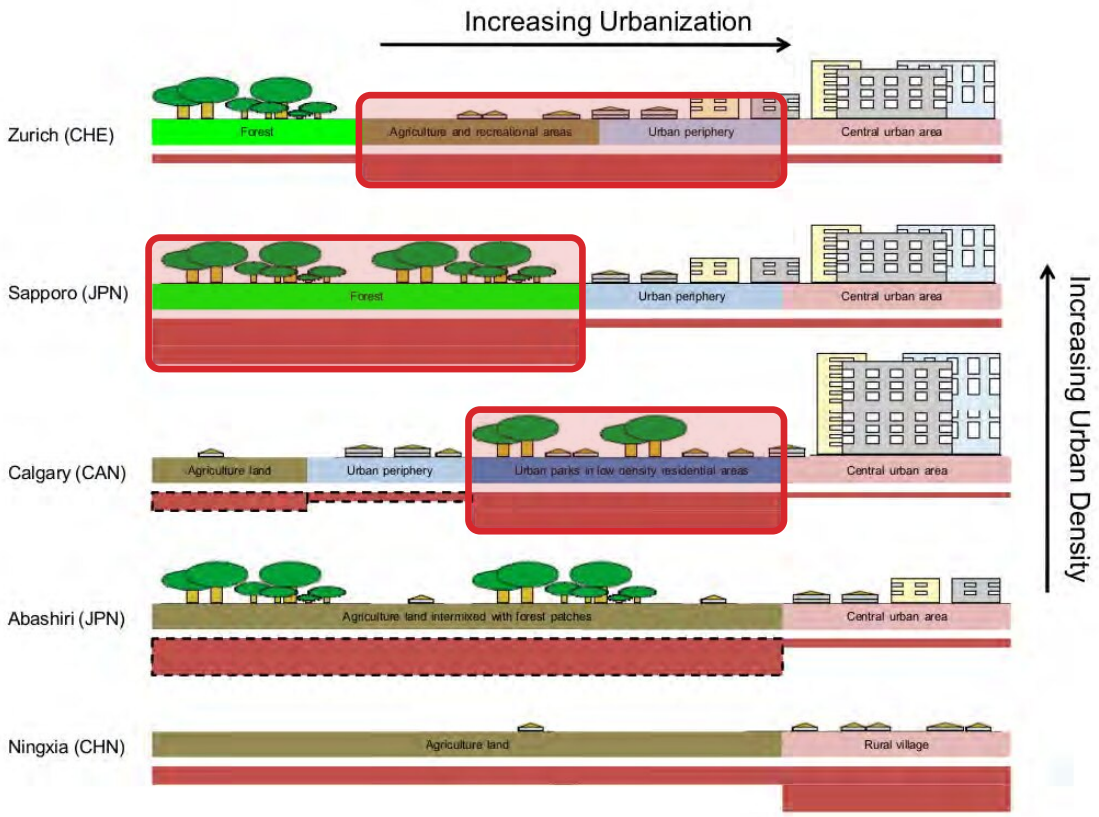
SAPPORO forest at the edge of the city

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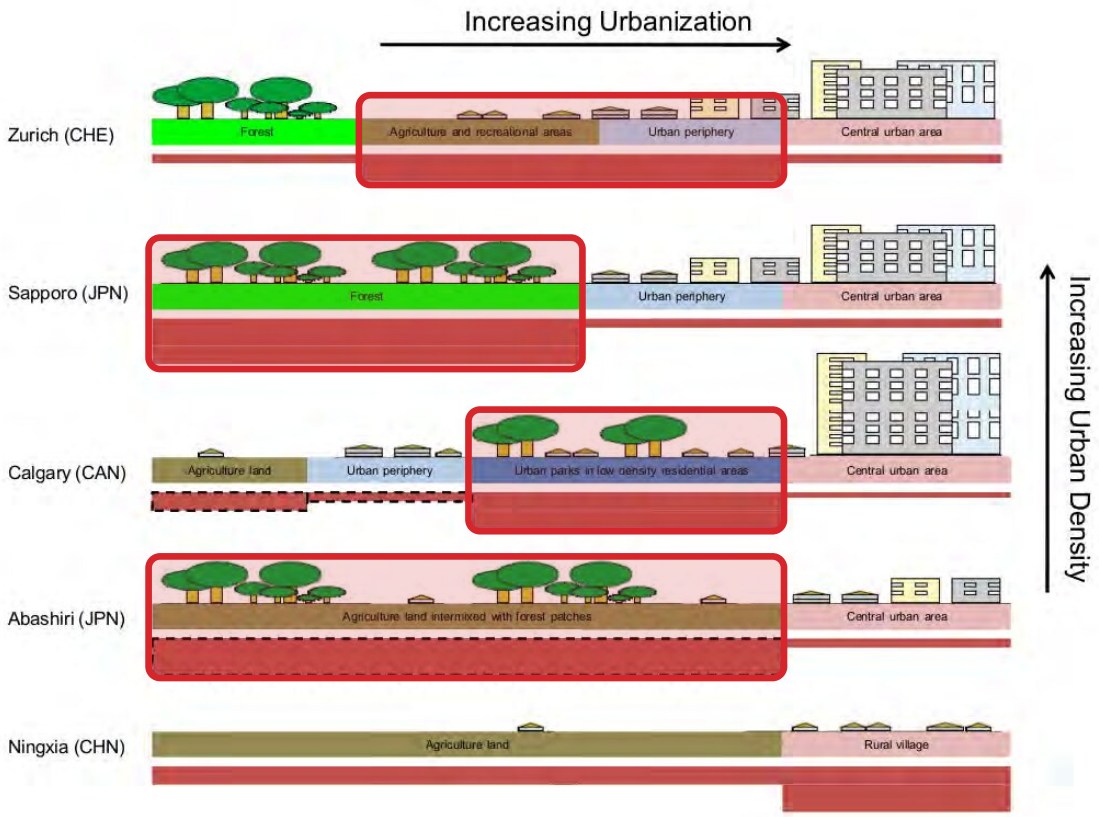
CALGARY urban parks in low-density residential areas

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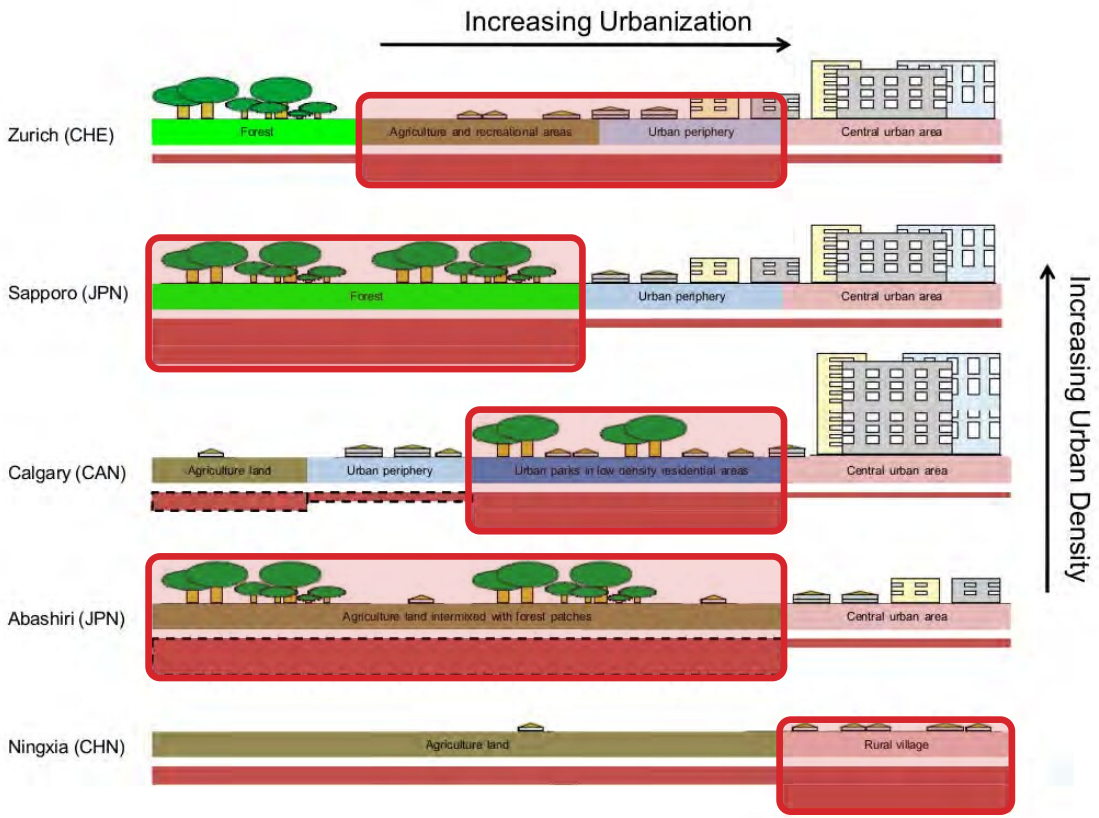
ABASHIRI agricultural land with forest patches (inferred)

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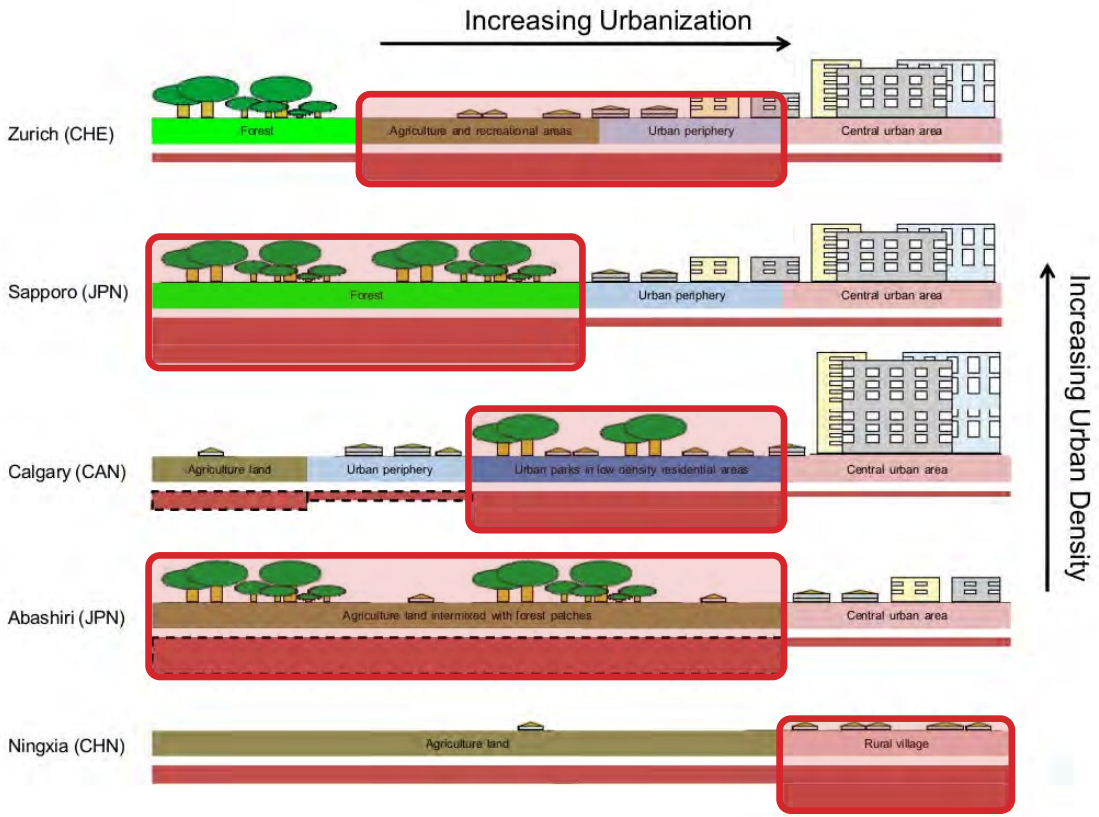
NINGXIA rural villages

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CALGARY urban parks in low-density residential areas

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NINGXIA rural villages

Everywhere: low in the central urban area

HOTSPOTS: COMPETENT VOLES + HEAVY PREDATOR USE

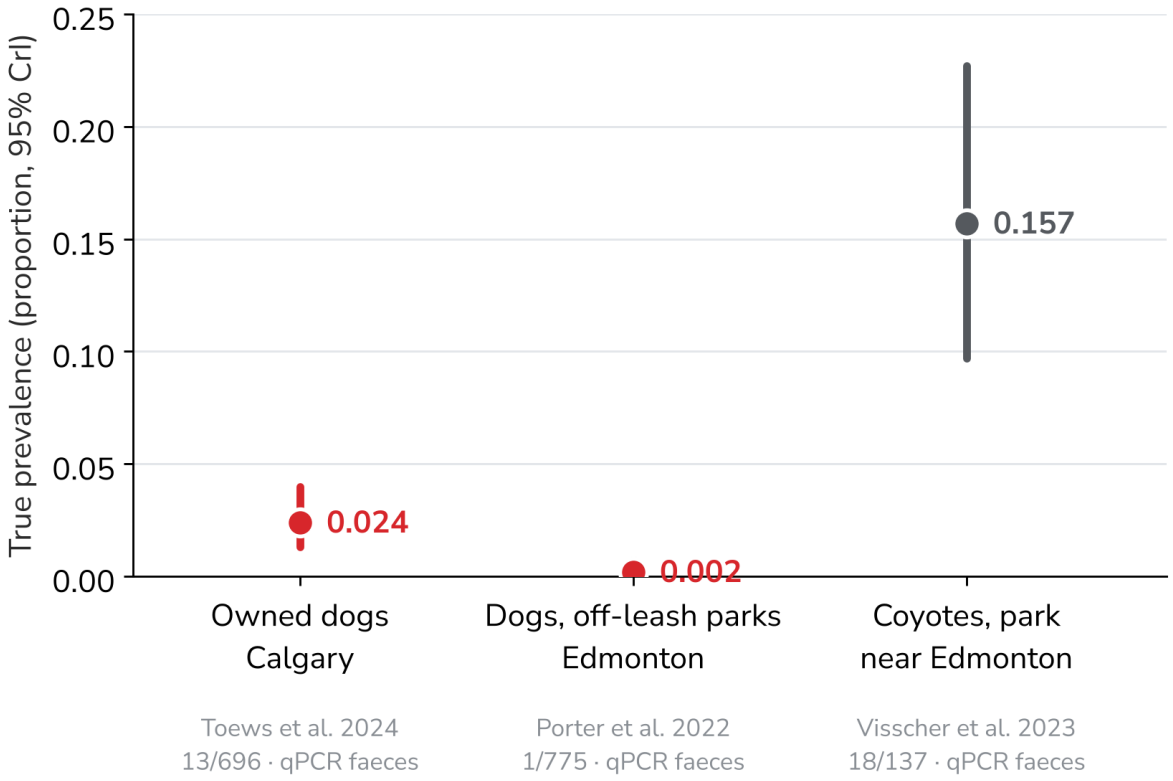
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DOGS: THE BRIDGE BETWEEN WILDLIFE AND PEOPLE

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DOGS: THE BRIDGE BETWEEN WILDLIFE AND PEOPLE

TRUE PREVALENCE IN ALBERTA

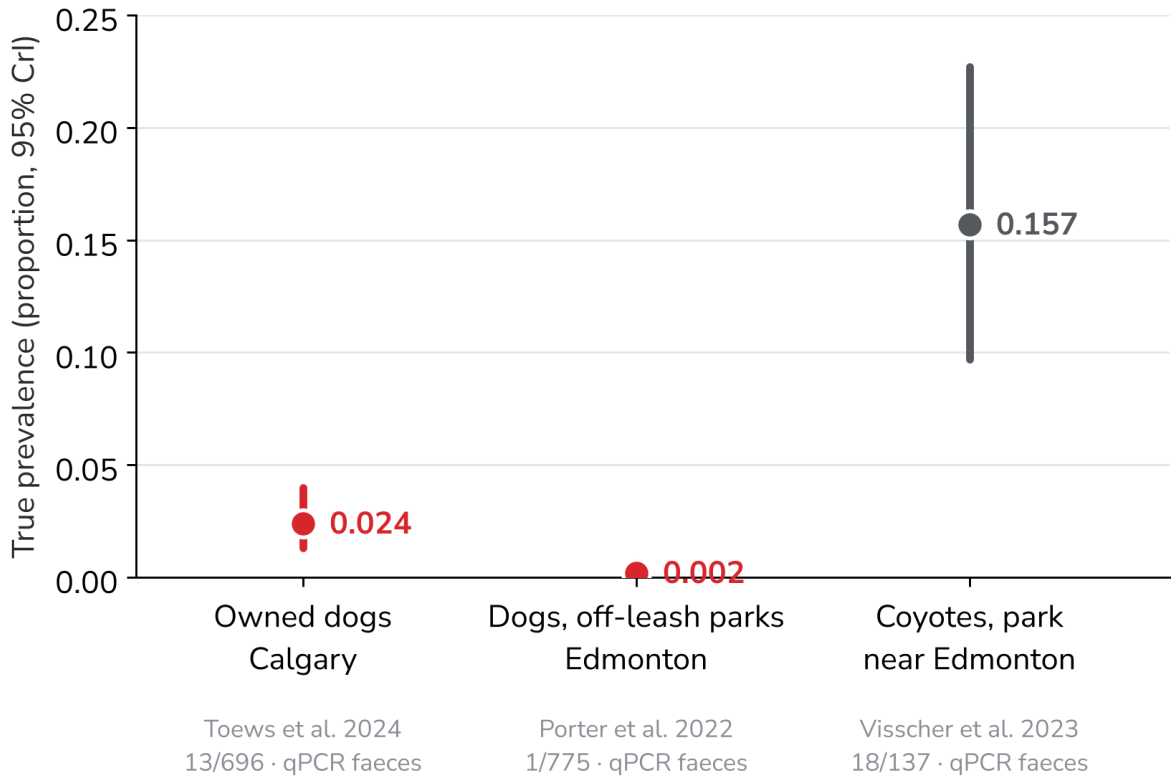


Bayesian true prevalence corrected for qPCR sensitivity and specificity, as reported in each paper

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DOGS: THE BRIDGE BETWEEN WILDLIFE AND PEOPLE

TRUE PREVALENCE IN ALBERTA



Bayesian true prevalence corrected for qPCR sensitivity and specificity, as reported in each paper

RISK FACTORS · OWNED DOGS, CALGARY

×5.6 hounds

×4.6 leashed at dog parks

×3.1 often in the backyard

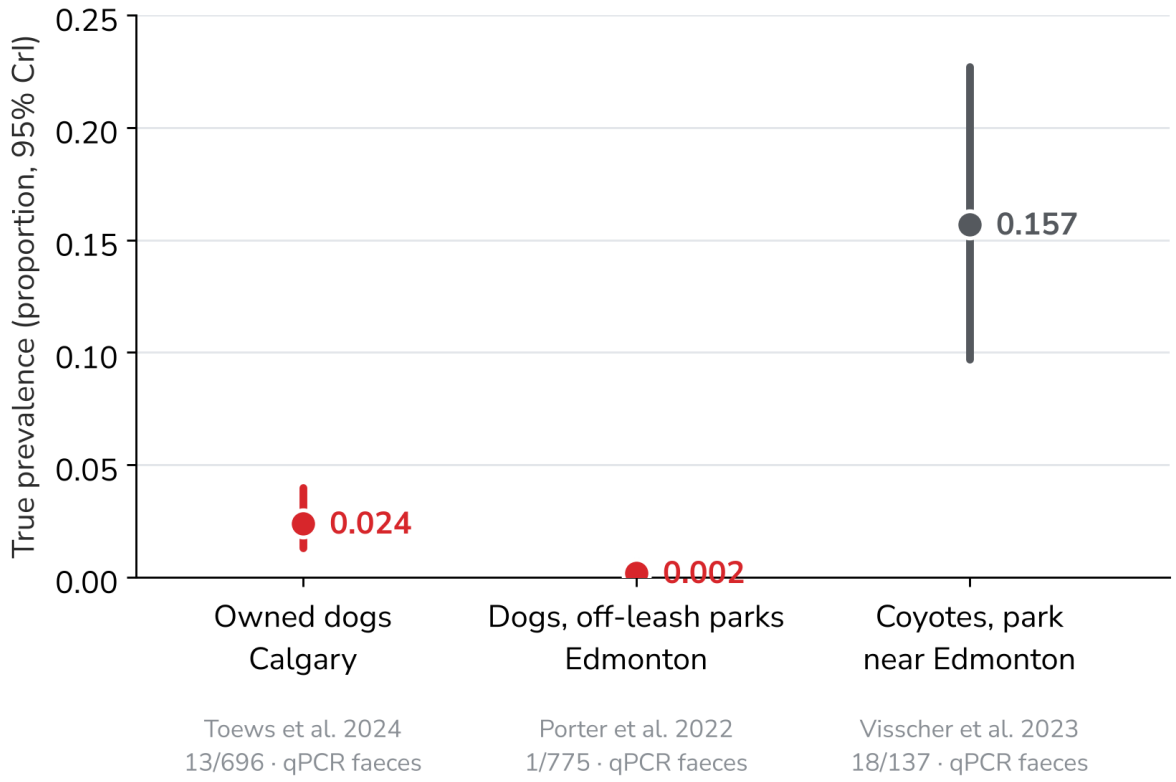
×3.3 living near Bowmont Park

Odds ratios; Toews et al. 2024, Sci Rep – same European strain as human cases (2 sequenced)

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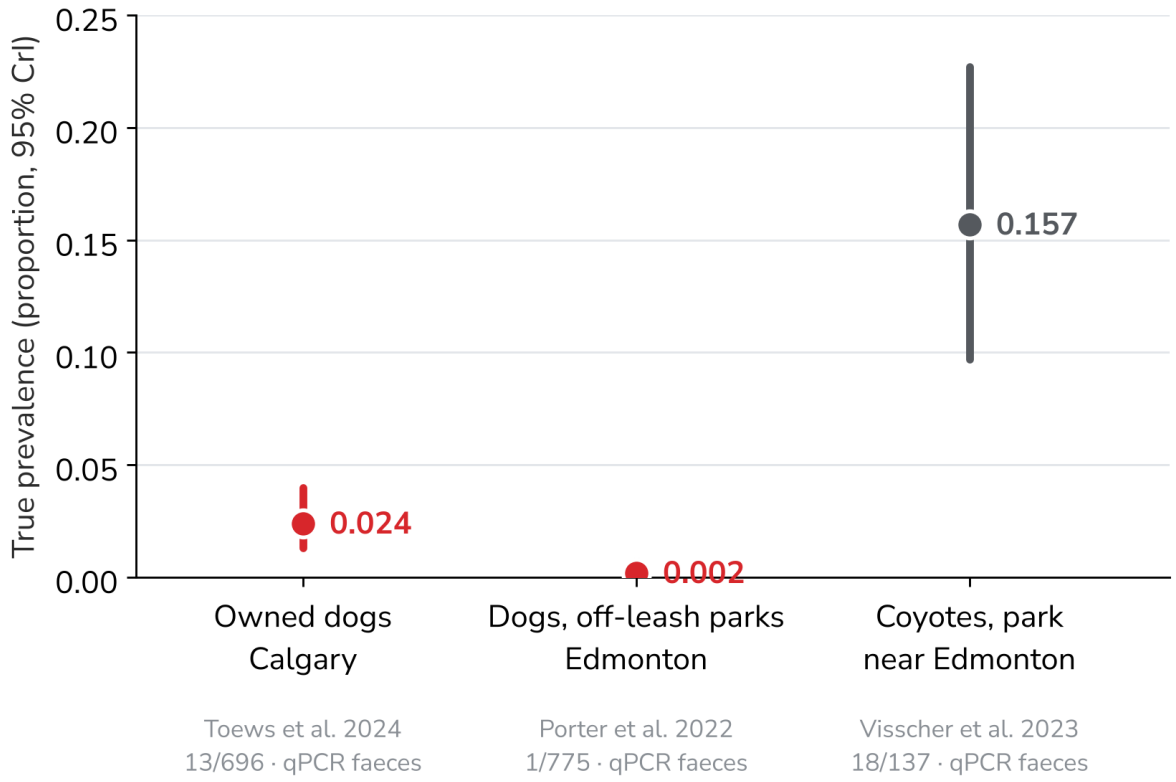
Coyote–human and coyote–dog temporal overlap rises in autumn–winter

Visscher et al. 2023, Front Parasitol – camera traps

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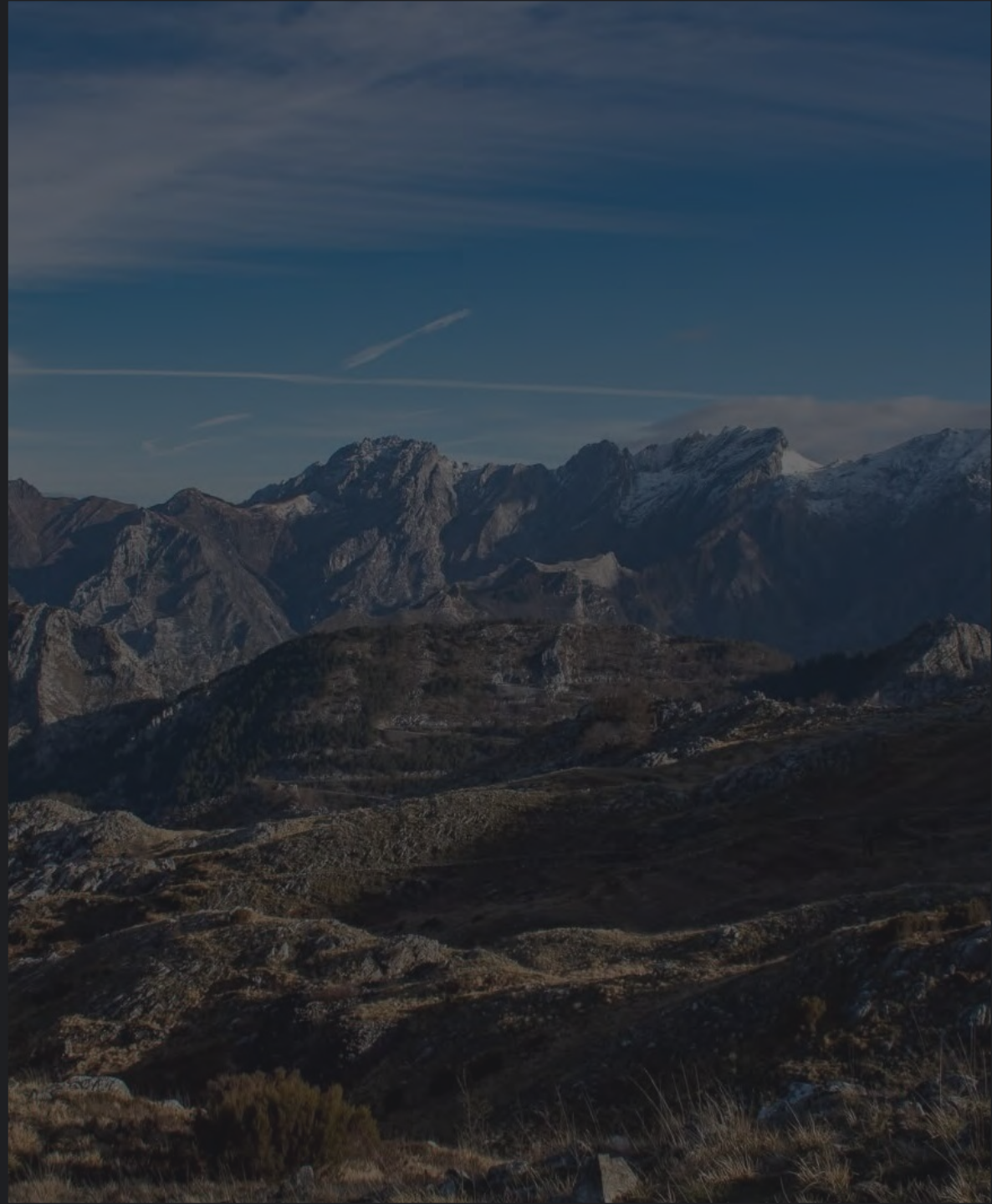
DOGS NEED SURVEILLANCE — AND DEWORMING POLICY

A Massolo, Dept. Biology, Univ. Pisa | alessandro.massolo@unipi.it

IV

SO WHAT FOR SURVEILLANCE?

From drivers to sampling decisions



A MULTI-SCALE MODEL OF EXPANSION

Synthesis from Simoncini & Massolo 2024, Food Waterborne Parasitol · Massolo et al. 2022, Trends Parasitol · Cenni et al. 2023, Glob Change Biol · Liccioli et al. 2015, Trends Parasitol · Santa et al. 2021, Parasitology · Santa et al. 2023, Proc R Soc B

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A MULTI-SCALE MODEL OF EXPANSION

CONTINENTAL	Cold-season temperature, humidity → egg survival; range of short-lived voles (bridge effect)

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CONTINENTAL	Cold-season temperature, humidity → egg survival; range of short-lived voles (bridge effect)
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PEOPLE, AT EVERY SCALE

Rabies vaccination · predator removal · feeding · urbanisation · translocation of dogs and foxes · climate change

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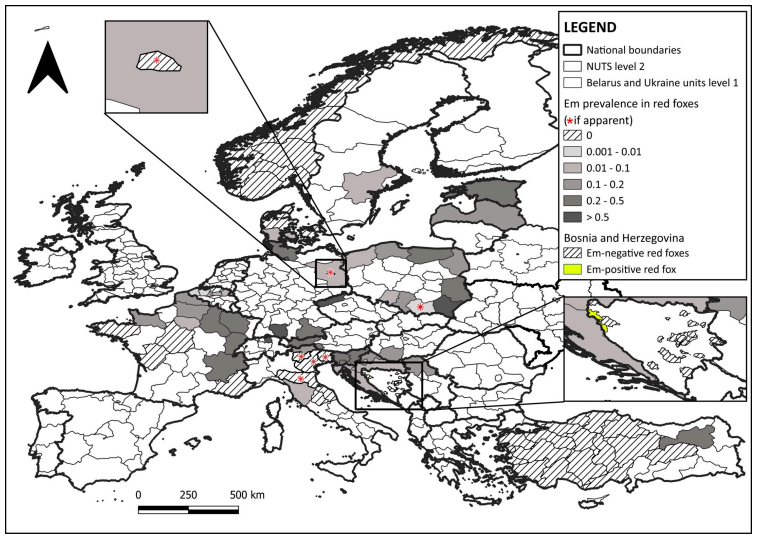
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THE CONSEQUENCE: A PATCHY PARASITE, AT EVERY SCALE

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THE CONSEQUENCE: A PATCHY PARASITE, AT EVERY SCALE

CONTINENT



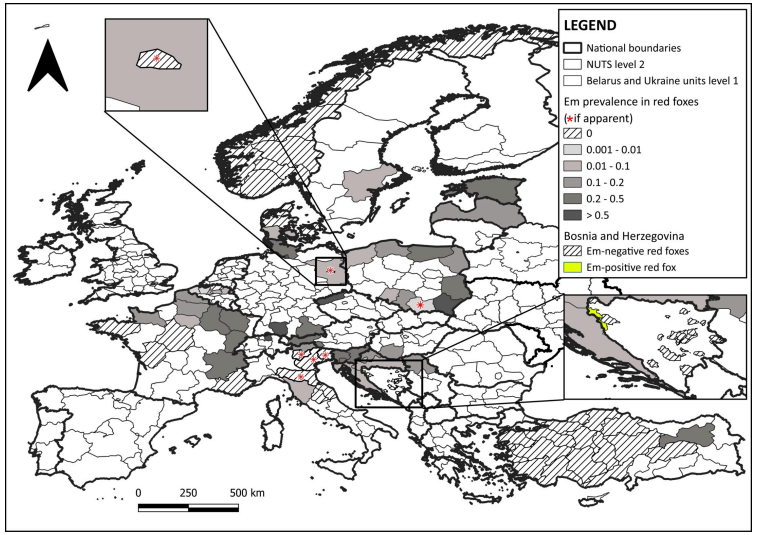
Neighbouring NUTS2 regions range from 0 to > 0.5 true prevalence in red foxes

Cafiero et al. 2026, Parasit Vectors

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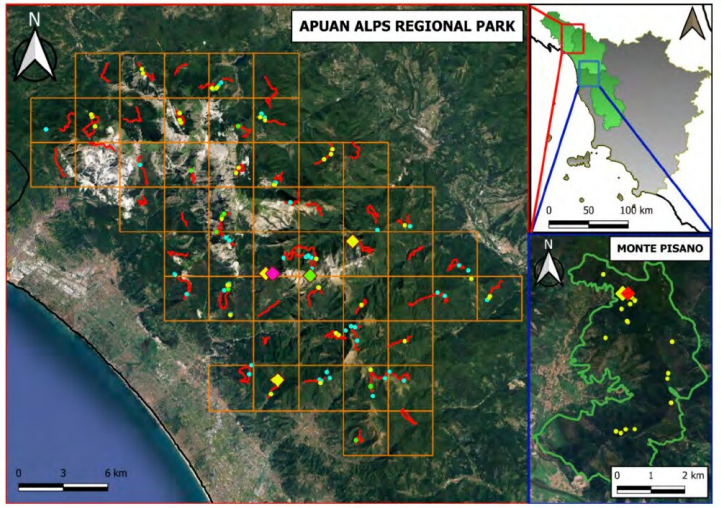
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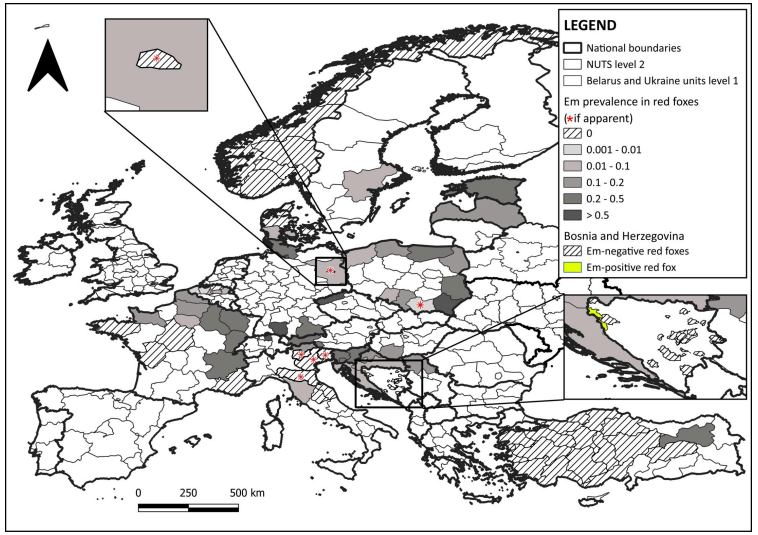
Positive canids a few hundred km beyond the nearest known focus

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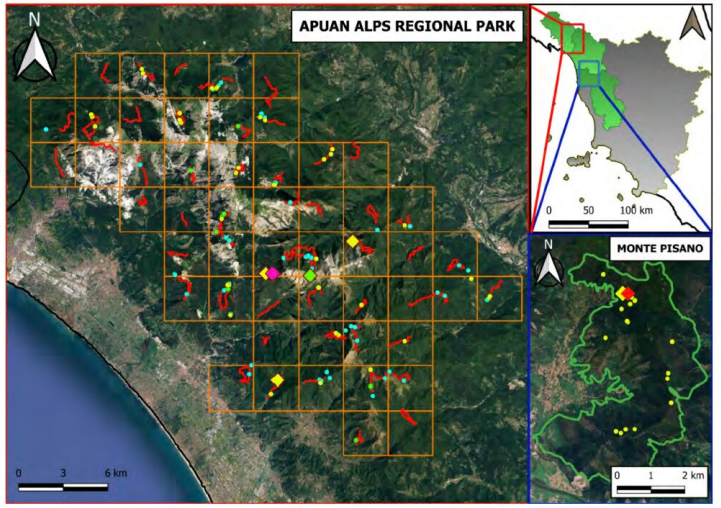
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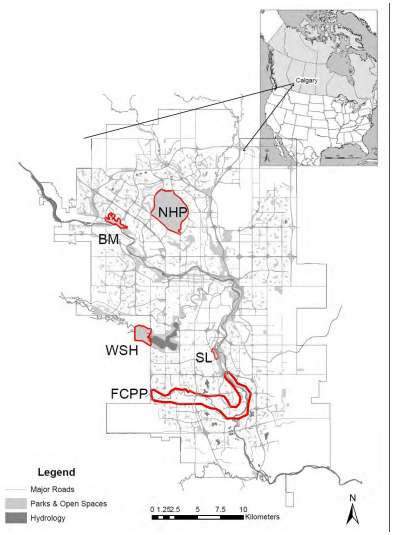
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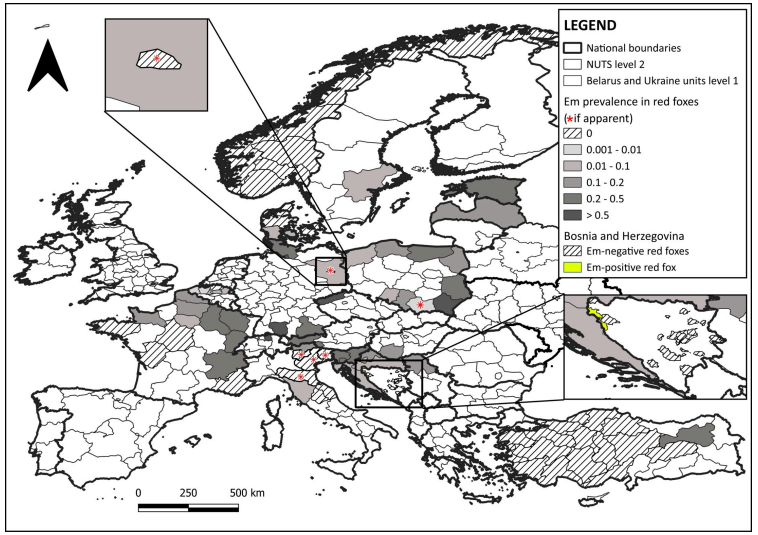
Apparent faecal prevalence in coyotes from 0.05 to 0.62 across parks of one city

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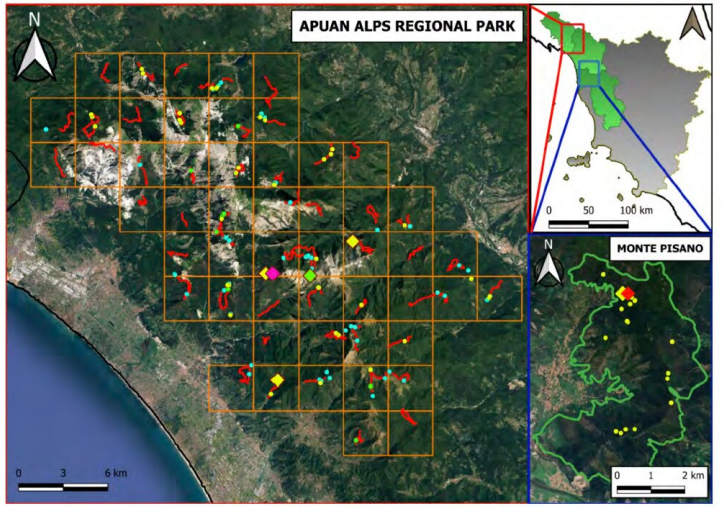
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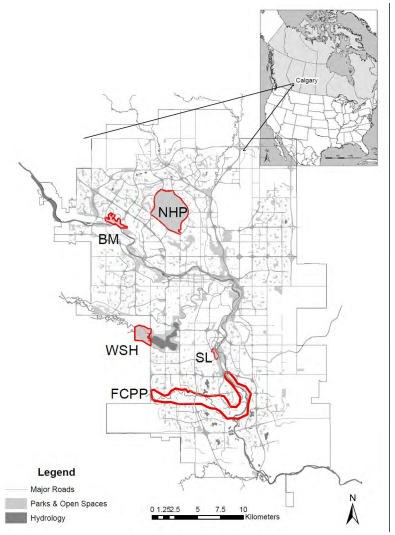
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RARE AND CLUSTERED: WHERE – AND HOW – DO WE SAMPLE?

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ADAPTIVE CLUSTER SAMPLING: FOLLOW THE POSITIVES

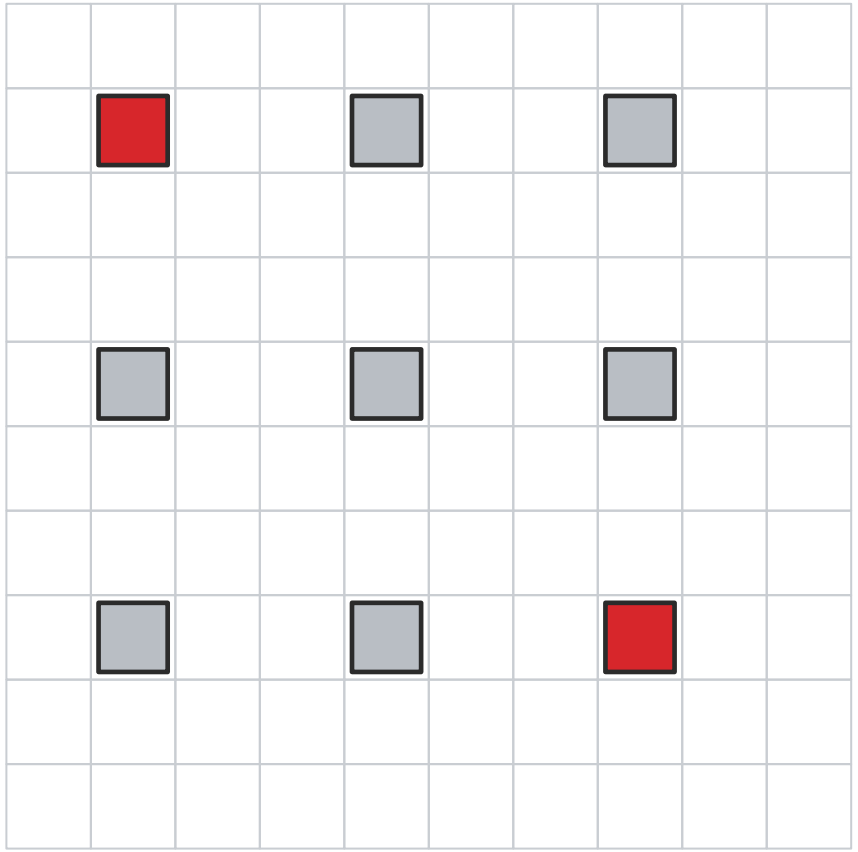
100 cells (e.g. 10 × 10 km each) · infected foxes are clustered

sampled, negative sampled, positive true infected area (hidden)

Thompson 1990, J Am Stat Assoc – adaptive cluster sampling; unbiased prevalence needs design-based (e.g. modified Horvitz–Thompson) estimators

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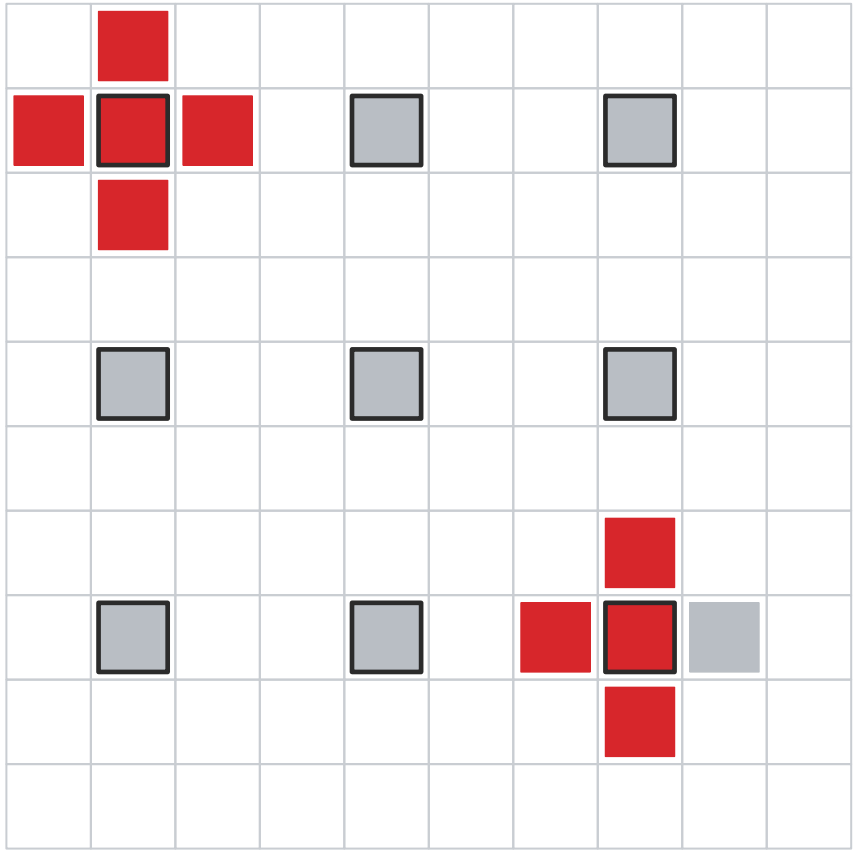
1 START SYSTEMATIC

Sample a regular grid of cells: 9 cells, 2 positive

Thompson 1990, J Am Stat Assoc – adaptive cluster sampling; unbiased prevalence needs design-based (e.g. modified Horvitz–Thompson) estimators

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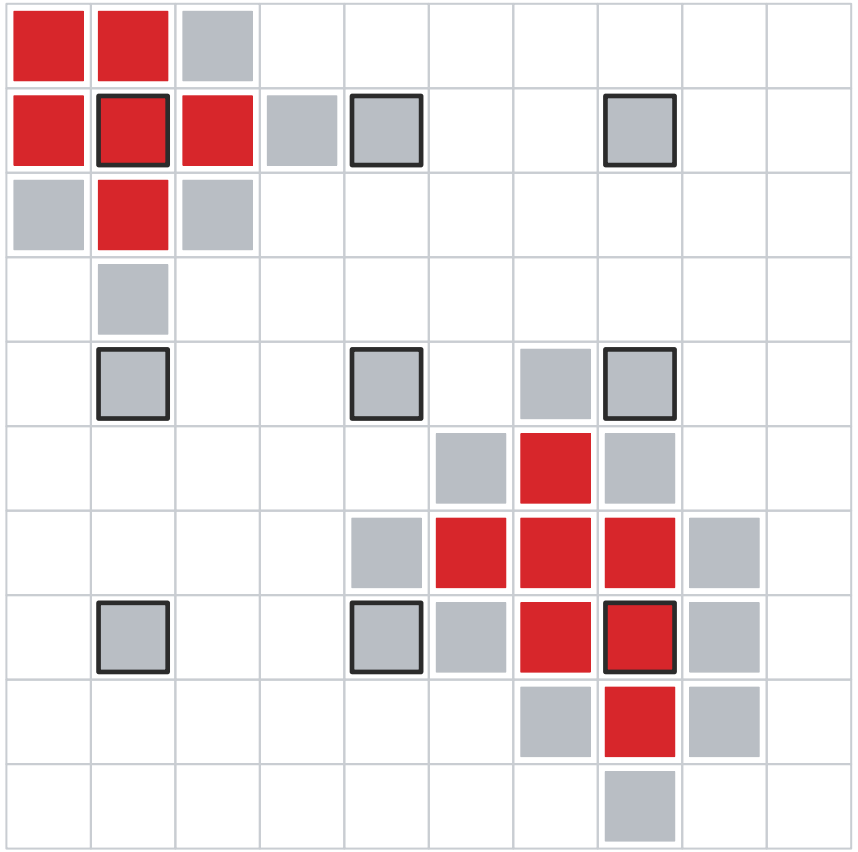
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For every positive cell, sample its 4 neighbours: 17 cells, 9 positive

Thompson 1990, J Am Stat Assoc – adaptive cluster sampling; unbiased prevalence needs design-based (e.g. modified Horvitz–Thompson) estimators

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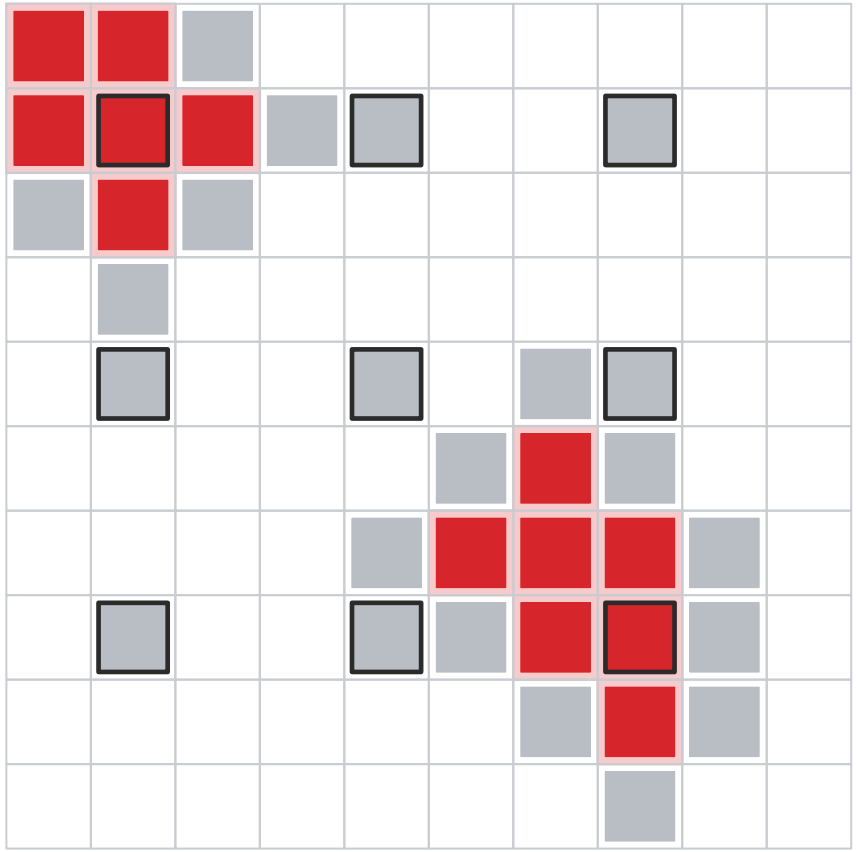
3 REPEAT UNTIL NO NEW POSITIVES

The edge of each cluster is drawn: 35 cells, 13 positive

Thompson 1990, J Am Stat Assoc – adaptive cluster sampling; unbiased prevalence needs design-based (e.g. modified Horvitz–Thompson) estimators

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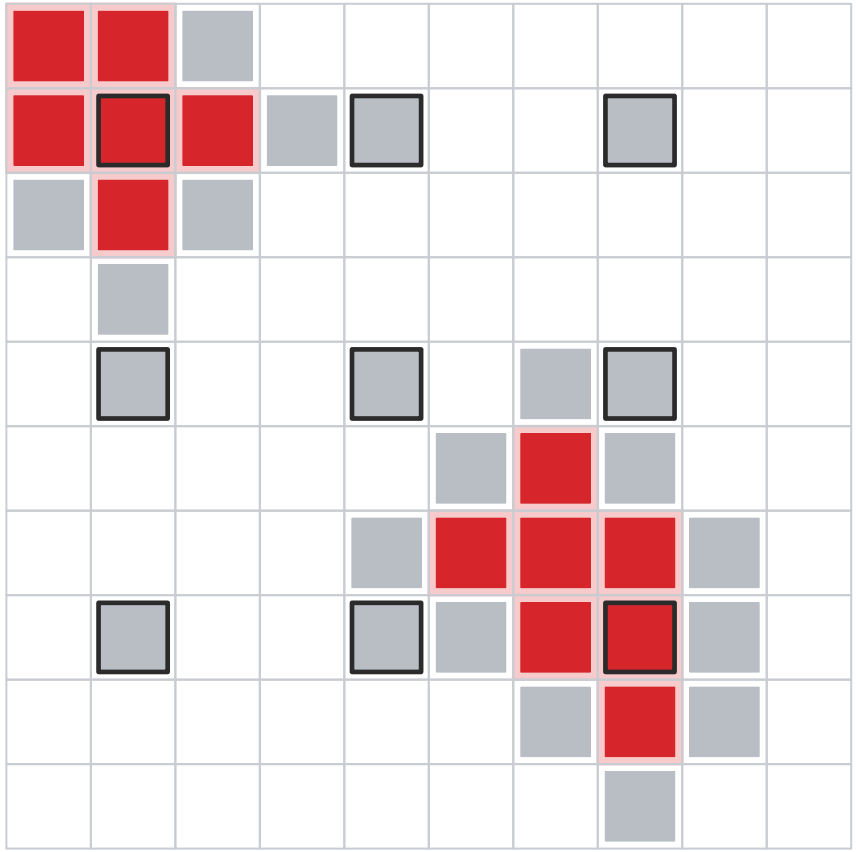
4 WHAT WAS THERE

Both clusters found and delineated — a fixed design of 35 cells would hit them only by chance

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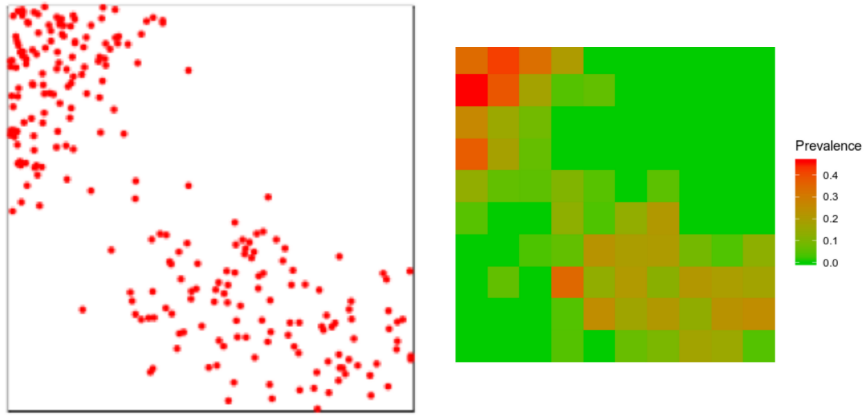
A DESIGN THAT LEARNS FROM WHAT IT FINDS

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ADAPTIVE vs SYSTEMATIC: SIMULATION RESULTS

SIMULATED LANDSCAPE · LOW DENSITY · PREVALENCE 0.1



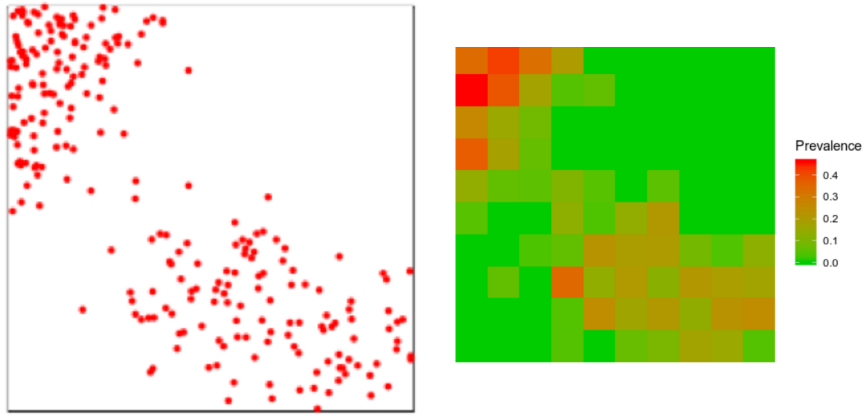
Clustered infected foxes (Matérn cluster process) → patchy prevalence across 100 cells of 10 × 10 km

Massolo & Giunchi, ICOPA 2018 – "Worm surveying", also at 14th NRL-P Workshop 2019; simulations in R (spatstat, TeachingSampling, epiR)

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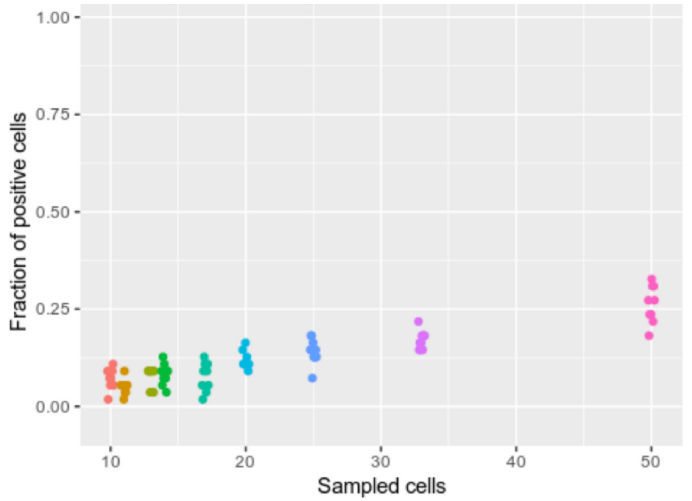
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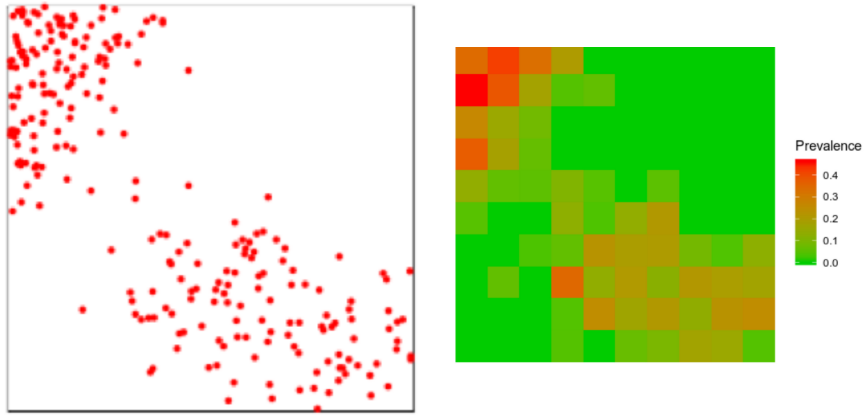
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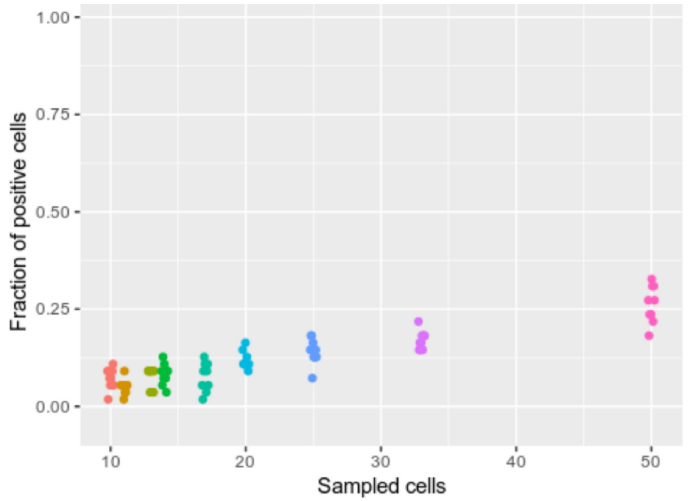
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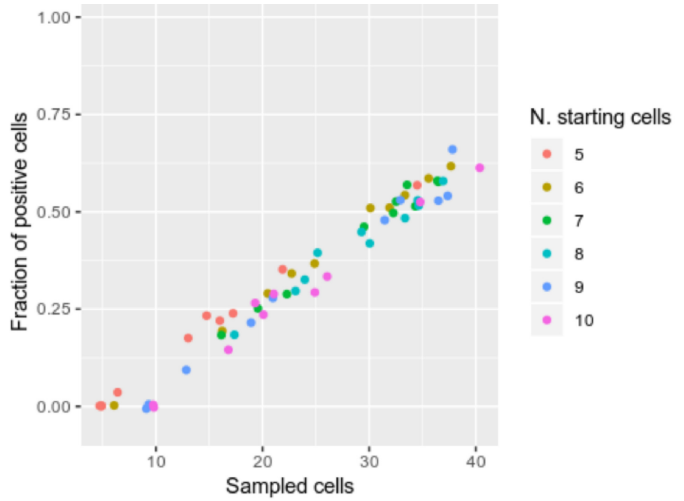


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ADAPTIVE



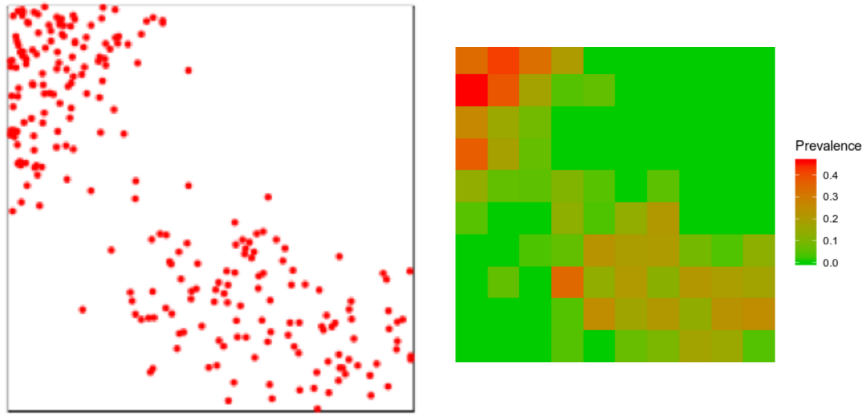
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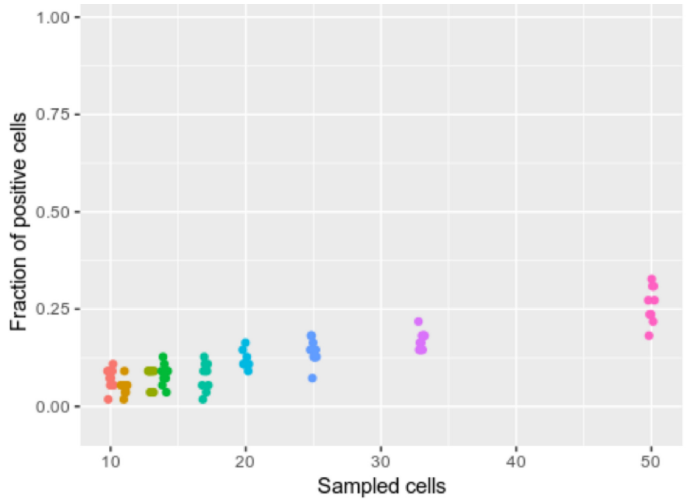
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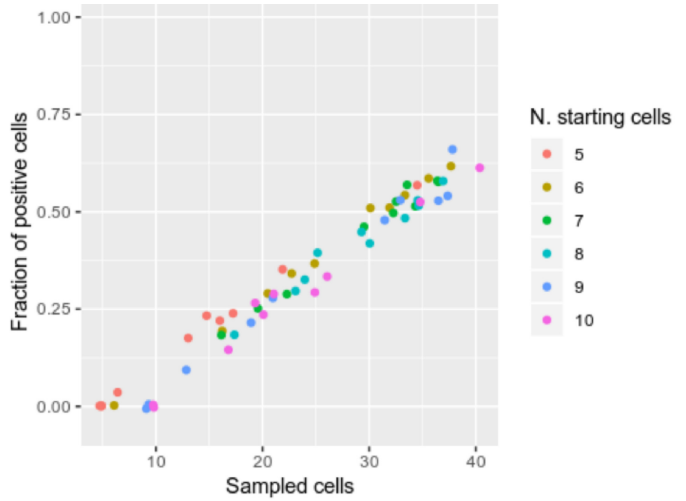


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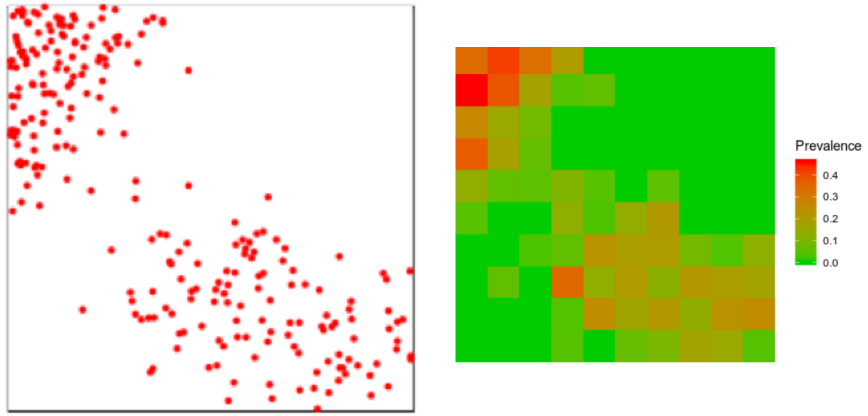
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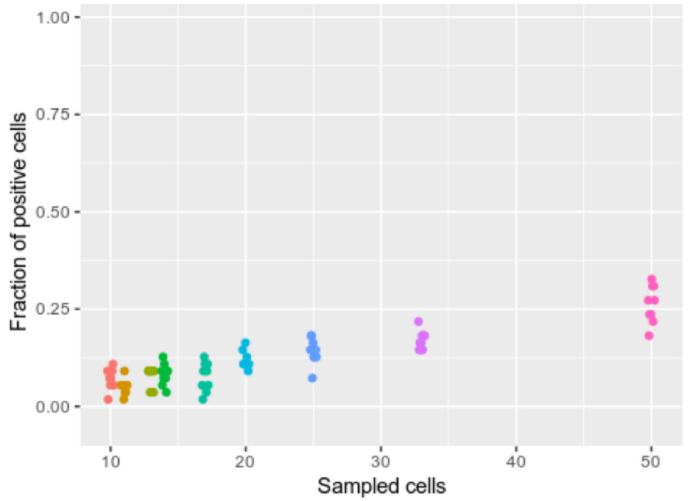
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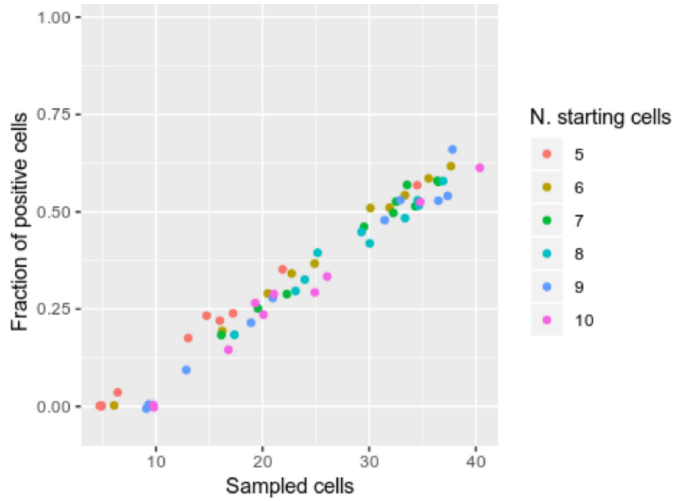


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SAME EFFORT, MORE FOCI FOUND

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NO ONE-SIZE-FITS-ALL DESIGN: ONE QUESTION, ONE DESIGN

Massolo & Giunchi, ICOPA 2018 · Blaker CIs: Reiczigel et al. 2010, Epidemiol Infect

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PREVALENCE IN DEFINITIVE HOSTS

Peak season (winter) · ~systematic grid · true prevalence with exact CIs for imperfect tests

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DETECTING FOCI AT LOW PREVALENCE

Adaptive cluster sampling from a systematic start

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Random cells: unbiased, but many false negatives – needs very large effort

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MANY SCALES, MANY QUESTIONS → MANY DESIGNS

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FOUR IMPLICATIONS FOR NATIONAL REFERENCE LABORATORIES

Cafiero et al. 2026, Parasit Vectors · Simoncini et al. 2025, Ecol Inform · Toews et al. 2021, Int J Parasitol · Santa et al. 2023, Proc R Soc B · Umhang et al. 2014, Infect Genet Evol

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Habitat suitability + predicted intermediate hosts; at edges, sample adaptively and follow the positives

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2 SAMPLE THE WHOLE GUILD

Jackals, wolves, raccoon dogs, dogs and cats; and intermediate hosts, to see the cycle, not just the fox

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True prevalence, known test Se/Sp, comparable spatial units: trends change with NUTS level

Cafiero et al. 2026, Parasit Vectors · Simoncini et al. 2025, Ecol Inform · Toews et al. 2021, Int J Parasitol · Santa et al. 2023, Proc R Soc B · Umhang et al. 2014, Infect Genet Evol

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4 GENOTYPE TO TELL SPREAD FROM INTRODUCTION

mtDNA haplotypes and EmsB in shared databases: local spread vs translocation of a new strain

Cafiero et al. 2026, Parasit Vectors · Simoncini et al. 2025, Ecol Inform · Toews et al. 2021, Int J Parasitol · Santa et al. 2023, Proc R Soc B · Umhang et al. 2014, Infect Genet Evol

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TAKE-HOME

TO TAKE HOME

TAKE-HOME

TO TAKE HOME

> The expansion of Em is a mosaic of local dynamics

TAKE-HOME

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TAKE-HOME

TO TAKE HOME

The expansion of Em is a mosaic of local dynamics

Each driver acts at its own scale — fox density is not enough

Surveillance must follow processes, not only maps

THANK YOU · QUESTIONS

"There is no single scale at which ecological phenomena should be studied" – Levin 1992, Ecology

S.A. Cafiero · L. Cenni · A. Simoncini · L. Colla · L. Petroni · M.A. Santa · S. Liccioli · K. Mori · E. Toews · D. Visscher · M. Musiani · K. Ruckstuhl · C. Klein · H.C. Hauffe · T. Romig · A. Casulli · D. Giunchi

Ethology Unit, Dept. Biology, University of Pisa · Faculty of Veterinary Medicine, University of Calgary · alessandro.massolo@unipi.it

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APPENDIX

DEEP DIVES

NUTS levels · Cafiero et al. 2026, Parasit Vectors · Simoncini & Massolo 2024, Food Waterborne Parasitol · Simoncini et al. 2025, Ecol Inform

WHAT ARE NUTS 1, 2 AND 3?

Nomenclature of Territorial Units for Statistics (Eurostat): a nested hierarchy of administrative regions used for EU statistics

LEVEL	WHAT IT IS	POPULATION	EU-27	EXAMPLE · TUSCANY	EXAMPLE · ALTO ADIGE	UNITS IN GLMM

Population thresholds and EU-27 counts (NUTS 2021): European Parliament fact sheet on NUTS; NUTS 2021 is the version used by Cafiero et al. 2026 · Units in GLMM: NUTS regions with red-fox data in Cafiero et al. 2026, Parasit Vectors

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NUTS 2	basic regions for regional policy (e.g. Italian regions, German Länder)	0.8–3 million	**242**	ITI1 · Toscana	ITH1 · Bolzano/Bozen	**72**

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NUTS 3	small regions (provinces, départements, districts)	150,000–800,000	**1,166**	ITI12 · Lucca (Apuan Alps)	ITH10 · Bolzano/Bozen	**114**

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In Alto Adige NUTS 2 and NUTS 3 coincide; in small countries all levels can coincide (e.g. Luxembourg)

ADMINISTRATIVE UNITS, NOT ECOLOGICAL ONES: THE ANSWER CAN CHANGE WITH THE UNIT

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CAFIERO ET AL. 2026 · HOW THE UPDATE WAS BUILT

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1,751	records (Web of Science 1,045 · Scopus 322 · PubMed 384)
1,246	after removing 505 duplicates
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Cafiero et al. 2026, Parasit Vectors (Fig. 1, PRISMA) – papers published 12 Feb 2015 – 31 Dec 2025

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WHAT THE 88 PAPERS CONTAIN

58	**26**	**19**
papers on red foxes only	other definitive hosts only	both red foxes and other hosts

Cafiero et al. 2026, Parasit Vectors (Results; Table 2)

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26 other definitive hosts only

19 both red foxes and other hosts

39 small intestines

29 faeces

15 both matrices

5 records with true prevalence in intermediate hosts

Sample sizes from a few animals to > 5,000; sampling periods from 1 month to 13 years

Cafiero et al. 2026, Parasit Vectors (Results; Table 2)

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FROM APPARENT TO TRUE PREVALENCE

True prevalence

$$TP = (AP + Sp - 1) / (Se + Sp - 1)$$

AP = apparent prevalence · Se = sensitivity · Sp = specificity of the test used · 95% CI by Blaker's method

Rogan & Gladen 1978, Am J Epidemiol · Reiczigel et al. 2010, Epidemiol Infect · applied in Cafiero et al. 2026, Parasit Vectors

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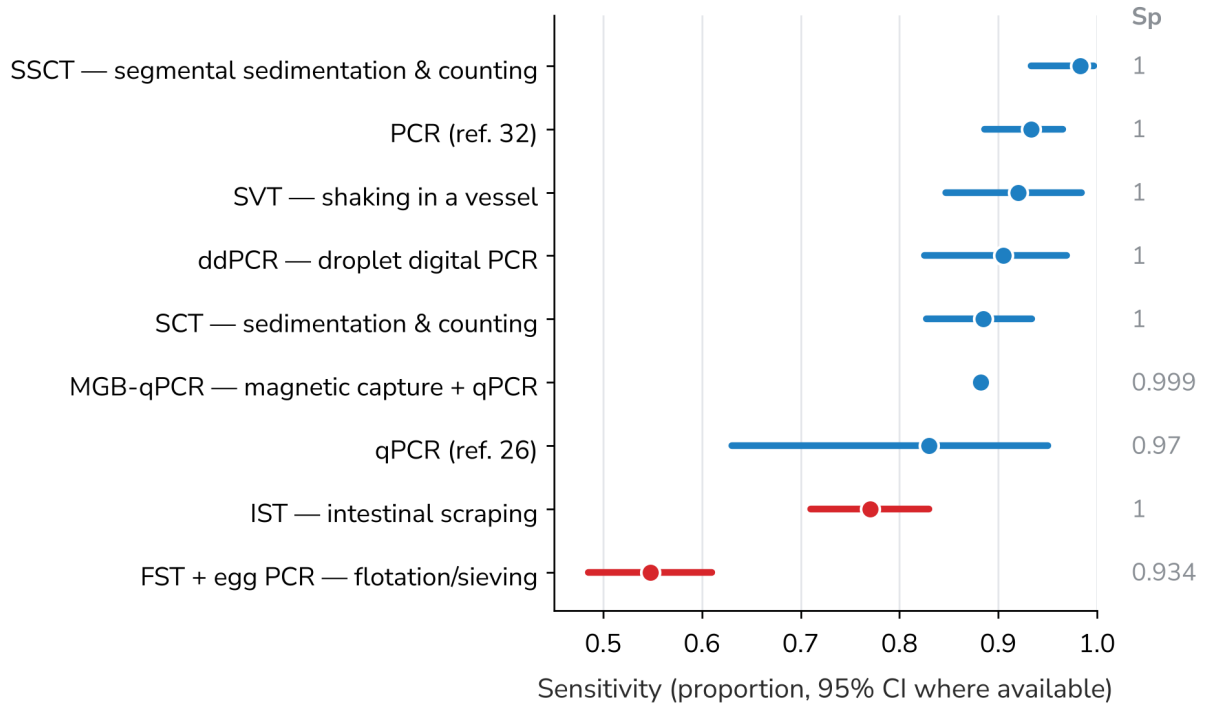
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DIAGNOSTIC PERFORMANCE USED FOR THE CORRECTION



Se and Sp values: Table 1 in Cafiero et al. 2026, Parasit Vectors (original sources cited there); when several estimates exist, one shown

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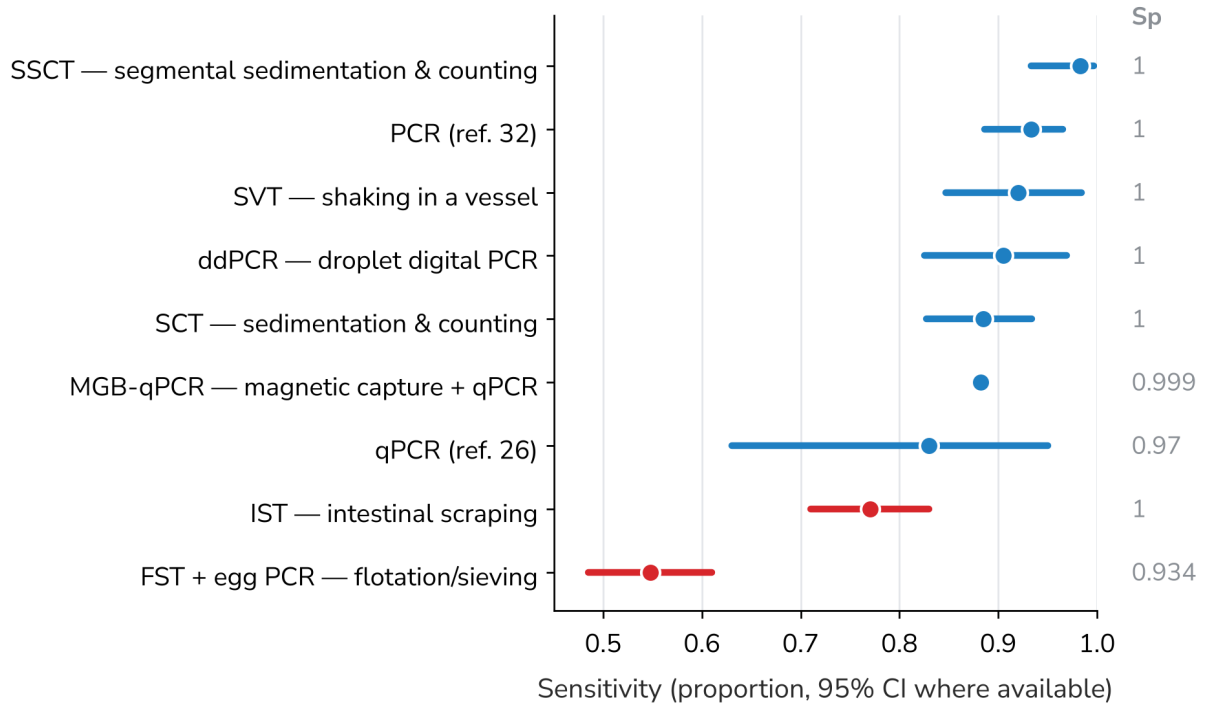
WORKED EXAMPLES · AP = 0.10

SCT Se 0.885, Sp 1 → TP = **0.113**

FST + egg PCR Se 0.548, Sp 0.934 → TP = **0.071**

With Sp < 1 the correction can go down, not only up

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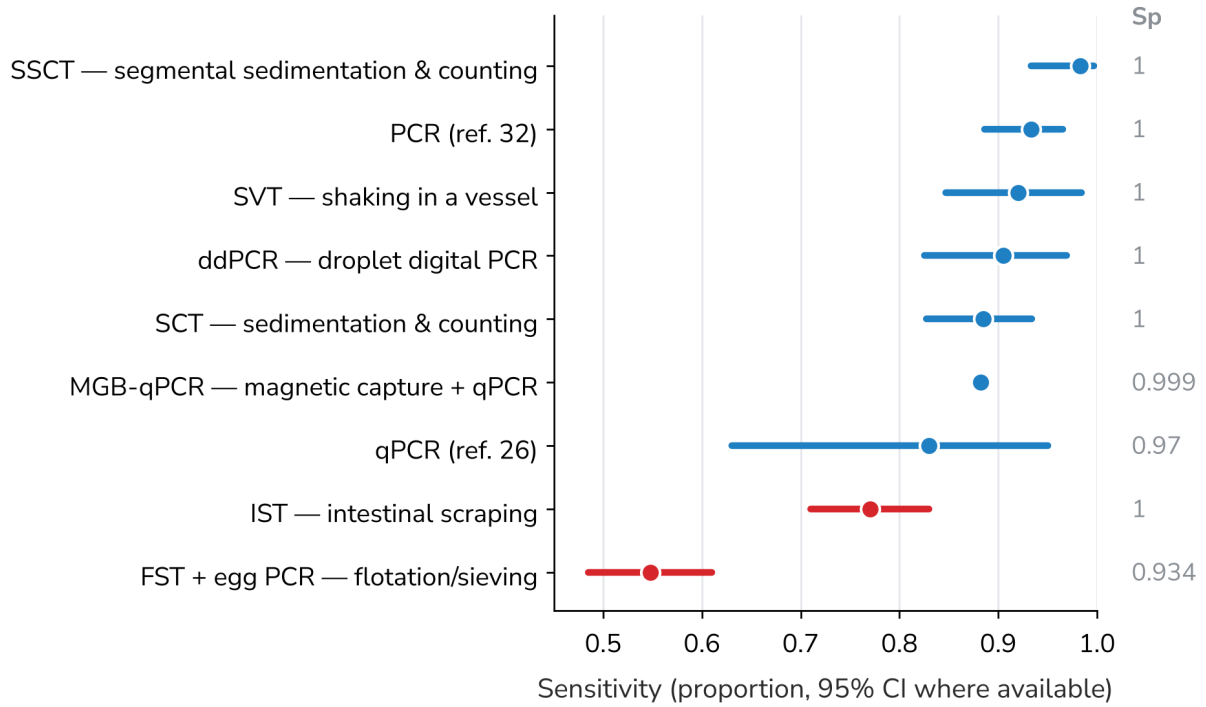
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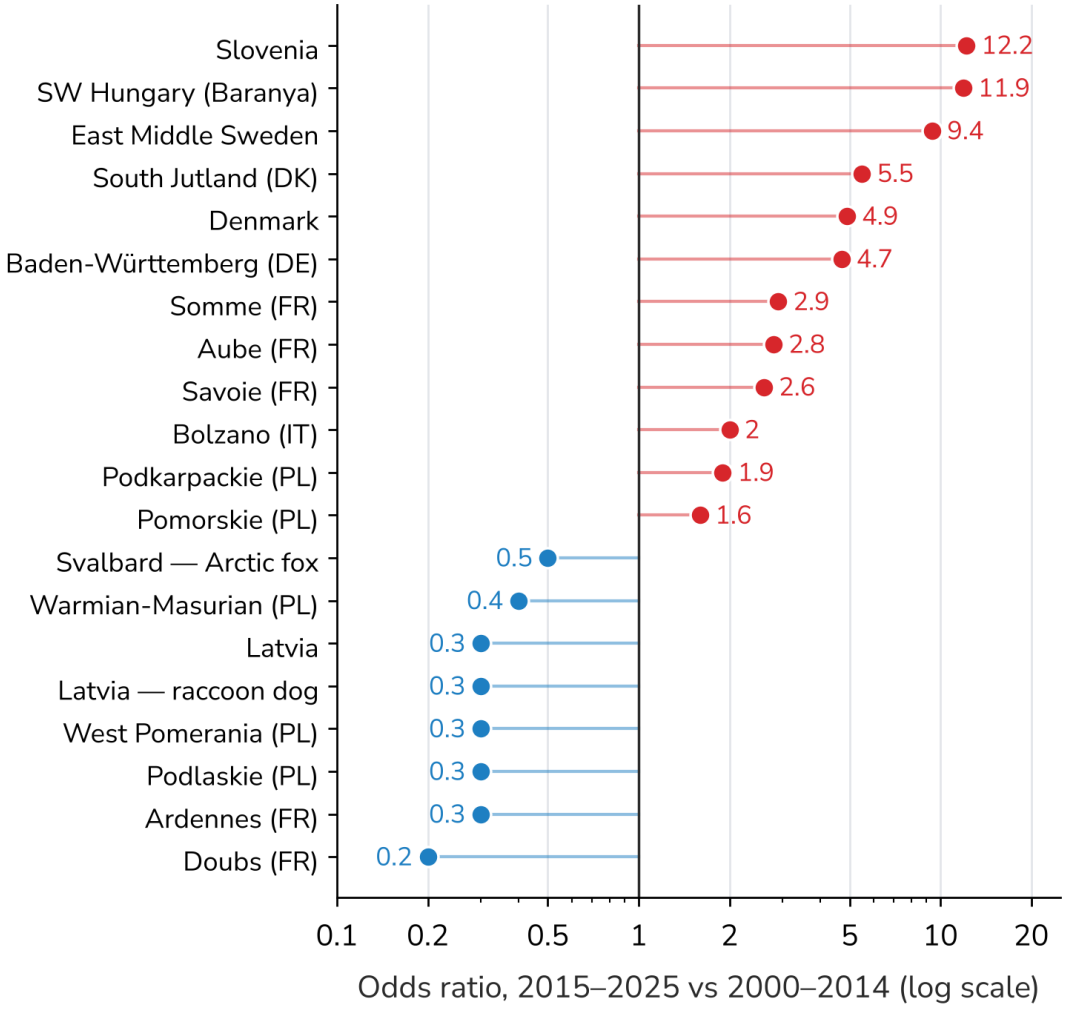


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WITHOUT CORRECTION, DIFFERENT TESTS MAKE DIFFERENT EPIDEMICS

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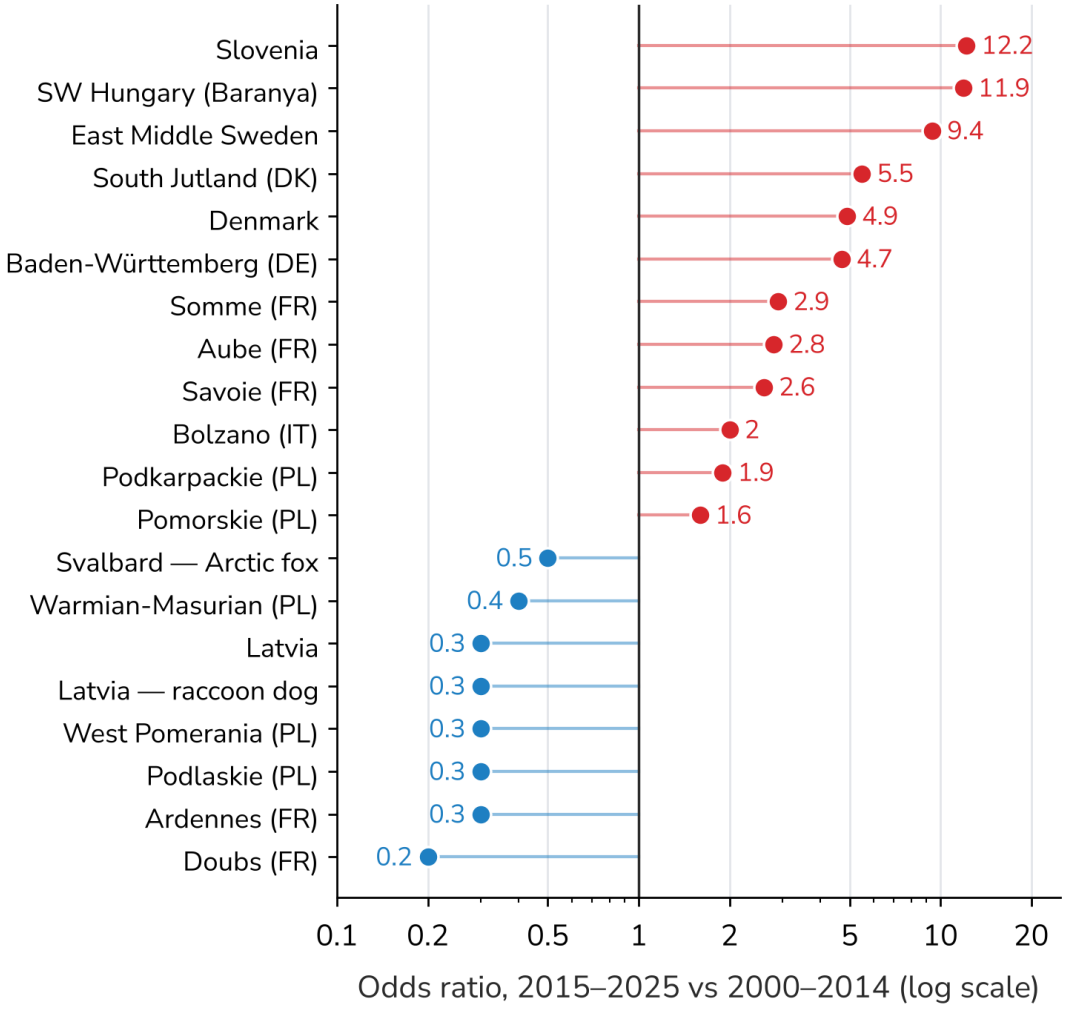
WHERE PREVALENCE CHANGED: 2015–2025 vs 2000–2014



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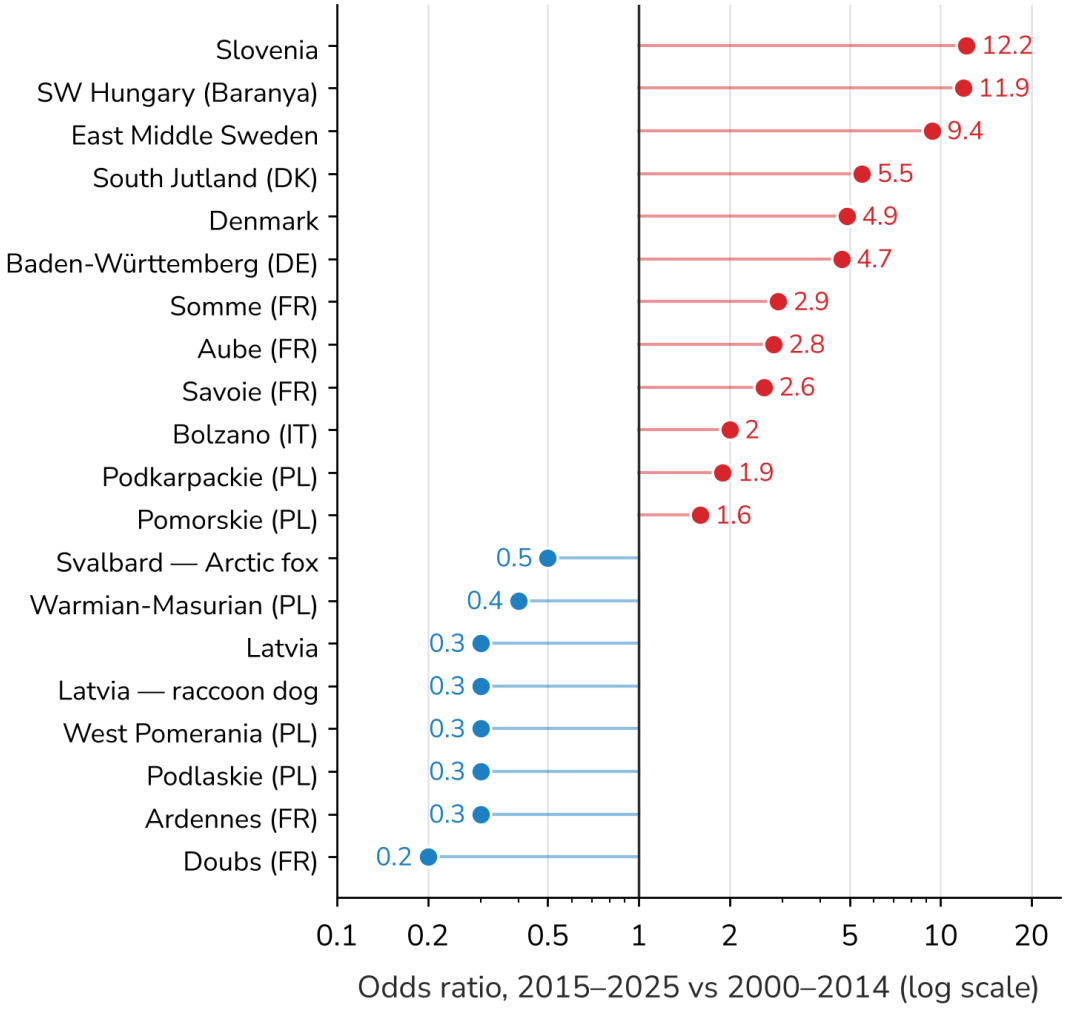
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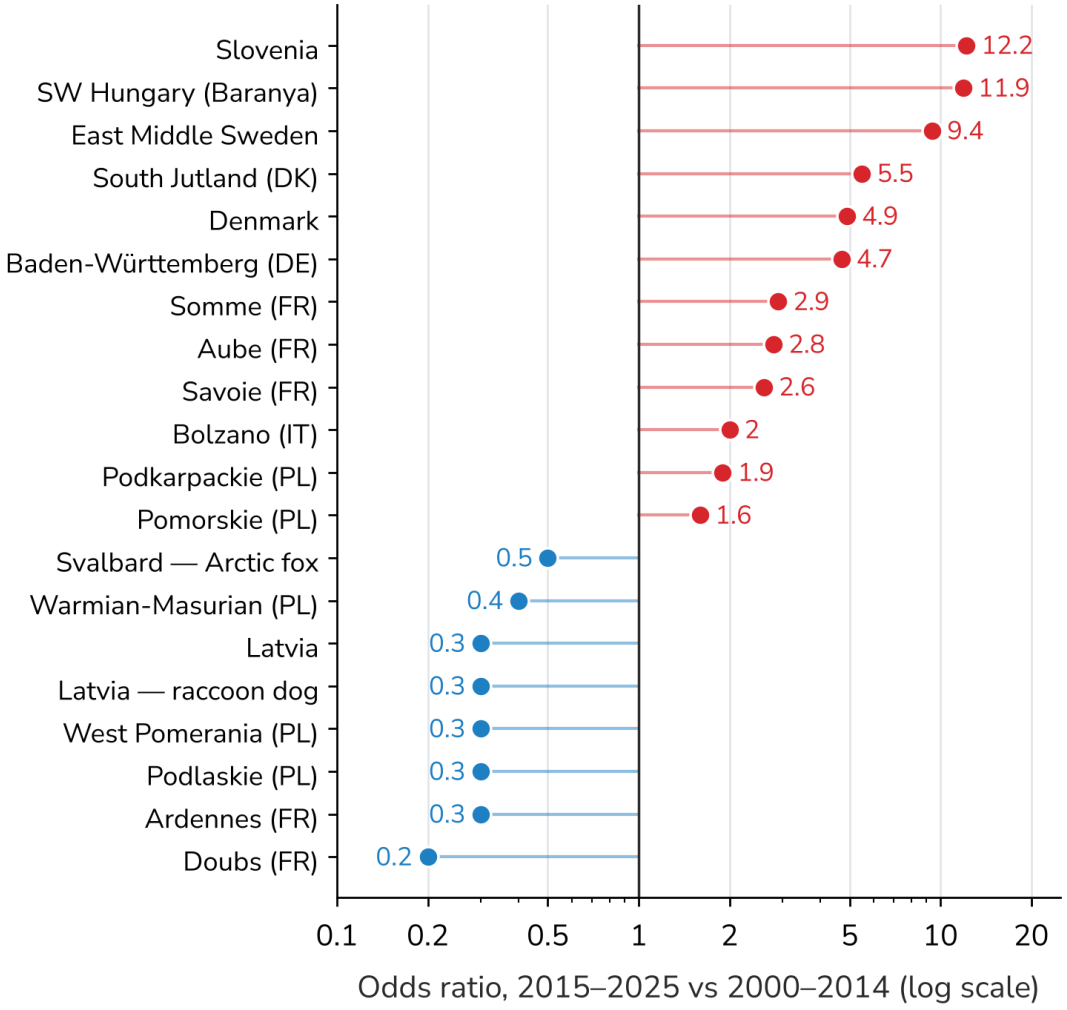
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INCREASES AND DECREASES SIDE BY SIDE, EVEN WITHIN ONE COUNTRY

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THE GLMMs: SAME DATA, THREE SPATIAL UNITS

$$y \sim \text{Binomial}(n, p) \cdot \text{logit}(p) = \beta 0 + \beta 1 \cdot \text{Period} + u(\text{NUTS})$$

Bayesian (brms); weakly informative priors; 4 chains × 20,000 iterations; fitted separately at each NUTS level; red-fox positives / tested; “Post” = 2015–2025 vs “Pre” = 2000–2014

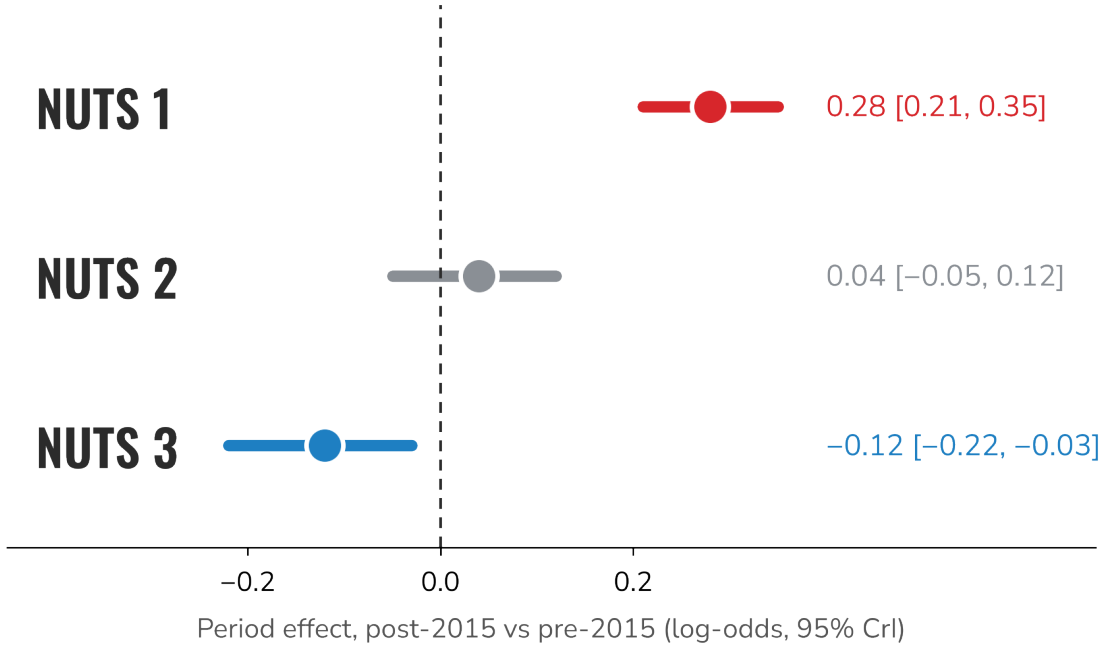
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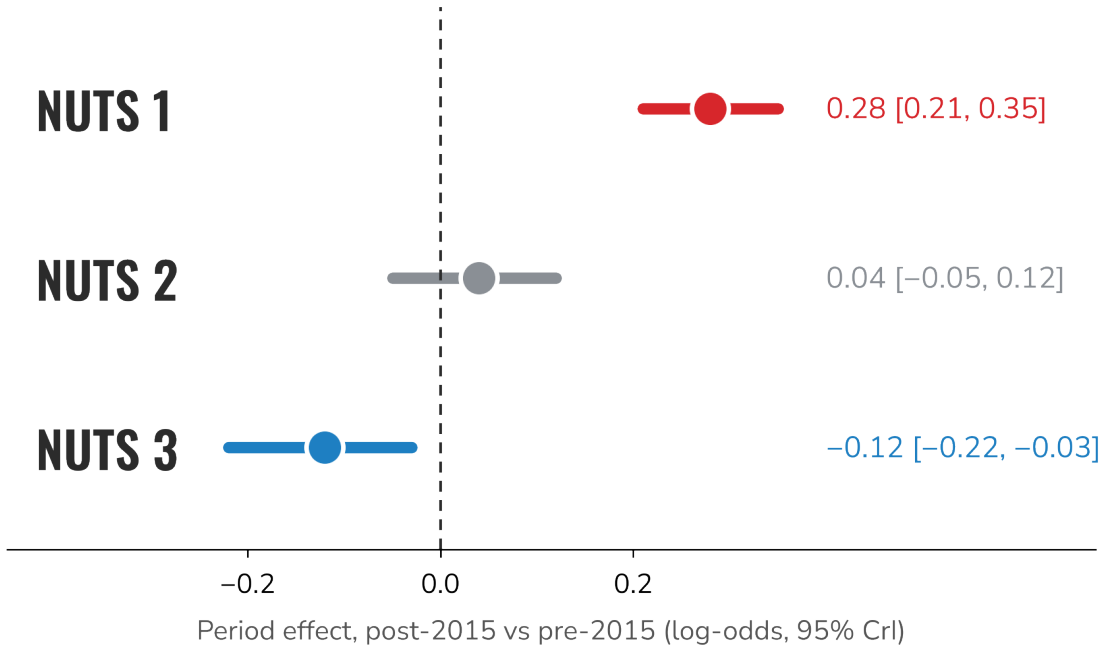


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NUTS 2	72	0.04 (−0.05–0.12)	2.72 (2.02–3.65)
NUTS 3	114	−0.12 (−0.22–−0.03)	2.50 (1.94–3.22)

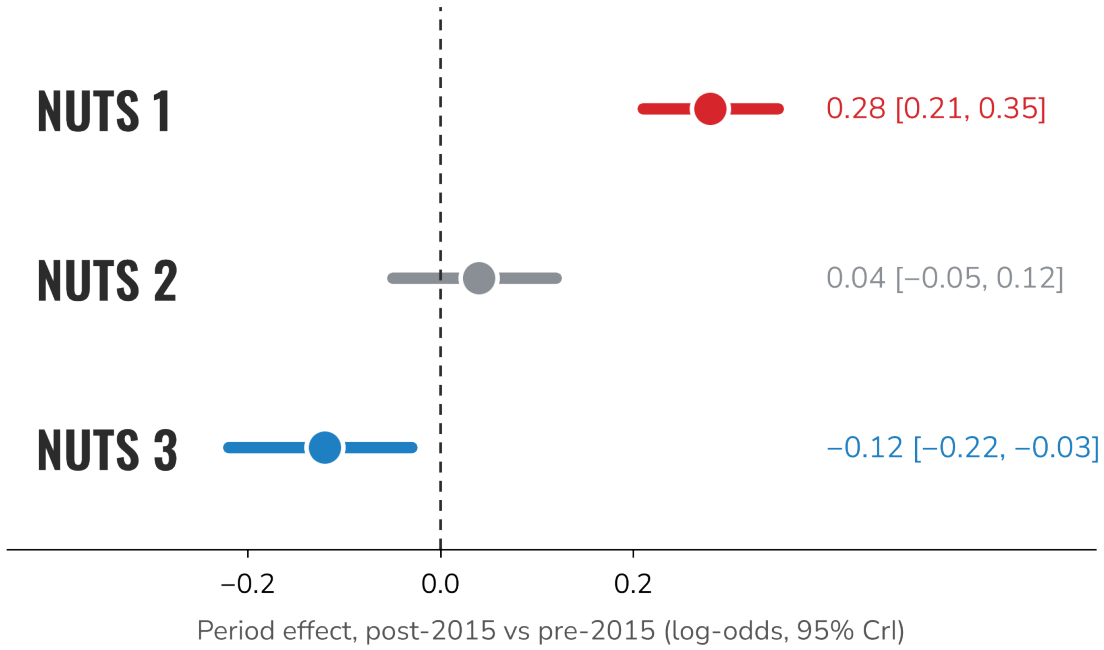
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σ NUTS ≈ 2.2–2.7 on the logit scale: between-region heterogeneity dwarfs the period effect

MODIFIABLE AREAL UNIT PROBLEM: AGGREGATION SHAPES INFERENCE

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CAFIERO ET AL. 2026 · WHAT WE STILL DO NOT KNOW

Cafiero et al. 2026, Parasit Vectors (Results; Discussion; Conclusions)

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Liechtenstein · Lithuania · Romania · Ukraine – endemic before 2015, no report since

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central Germany · Czech Republic (most) · Switzerland (most) · eastern Hungary · Luxembourg · Slovakia · Belarus · Bulgaria · Estonia · Lithuania · Netherlands · Romania · Sweden (most) · Ukraine

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INTERMEDIATE HOSTS

Only 5 records with true prevalence; most IH studies histology-only — is the cycle locally complete at new edges?

Cafiero et al. 2026, Parasit Vectors (Results; Discussion; Conclusions)

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PRIORITY: SPATIALLY STANDARDISED SURVEILLANCE OF COMPETENT HOSTS

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SIMONCINI & MASSOLO 2024 · HOW THE REVIEW WAS BUILT

QUESTION

Which ecological drivers explain the spatial distribution and transmission of *E. multilocularis* in wild hosts – and at which scale?

Simoncini & Massolo 2024, Food Waterborne Parasitol (Methods; Results; Fig. 1; Tables 1–2) – scales: local, regional, country, continental

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SIMONCINI & MASSOLO 2024 · HOW THE REVIEW WAS BUILT

QUESTION

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1,724	records (Web of Science, Scopus, PubMed; search 26 June 2023)
1,039	screened after 685 duplicates
38	full texts assessed
23	studies included

Inclusion: Em detected in sylvatic hosts · spatial variation related to ecological drivers · location reported

Simoncini & Massolo 2024, Food Waterborne Parasitol (Methods; Results; Fig. 1; Tables 1–2) – scales: local, regional, country, continental

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WHAT THE 23 STUDIES COVER

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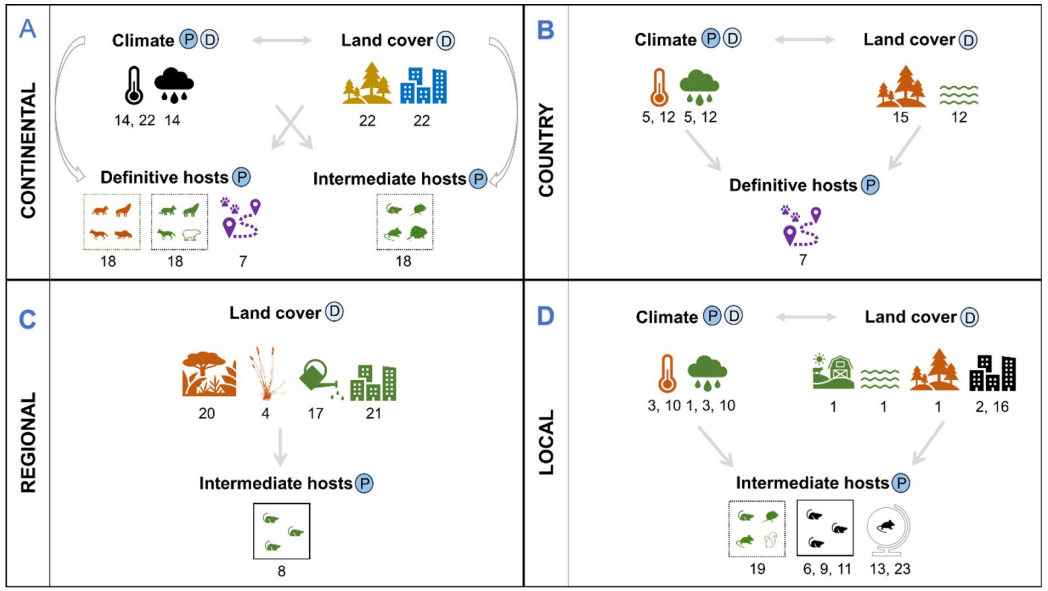
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Most studied (4 studies each): average temperature (negative) · average precipitation (positive) · urban cover (mostly positive)

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SIMONCINI & MASSOLO 2024 · CONSISTENT vs SCALE-DEPENDENT DRIVERS

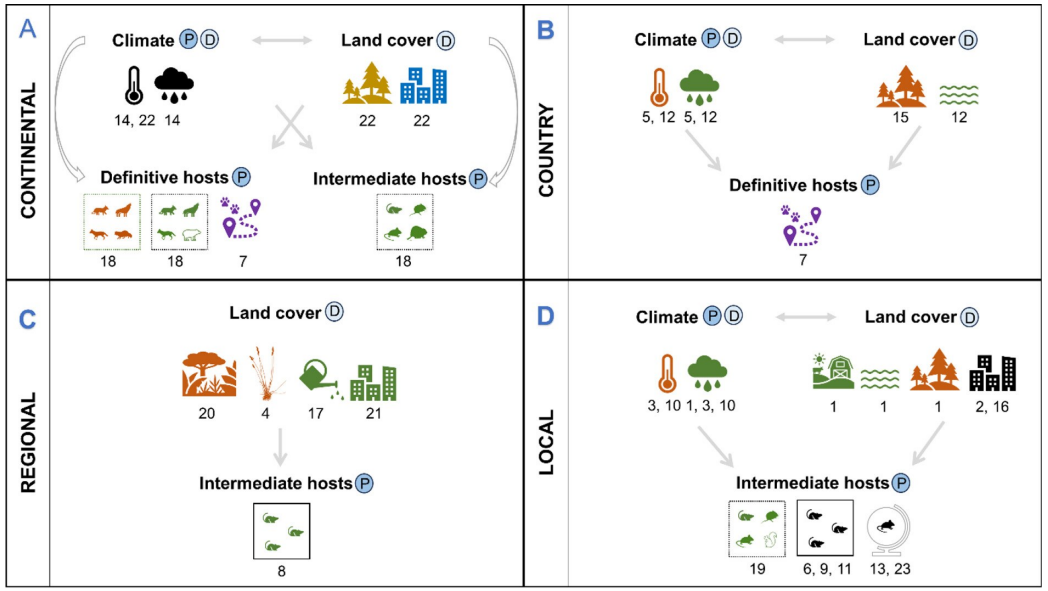


	Temperature		Pasture		DH density
	Precipitation/Humidity		Urban		DH proportion
	Water bodies		DH* dispersal		IH richness
	Kitchen gardens		IH** distribution	+ correlation	
	Natural habitat		DH density	- correlation	
	Forest		DH proportion	Unimodal	
	Grass		DH richness	Asymptotic	
				Other	
				More than one	
				P Proximal driver	
				D Distal driver	

*DH = Definitive Host, **IH = Intermediate Host

Figure and synthesis: Simoncini & Massolo 2024, Food Waterborne Parasitol (Fig. 2; sections 3, 4.7, 5)

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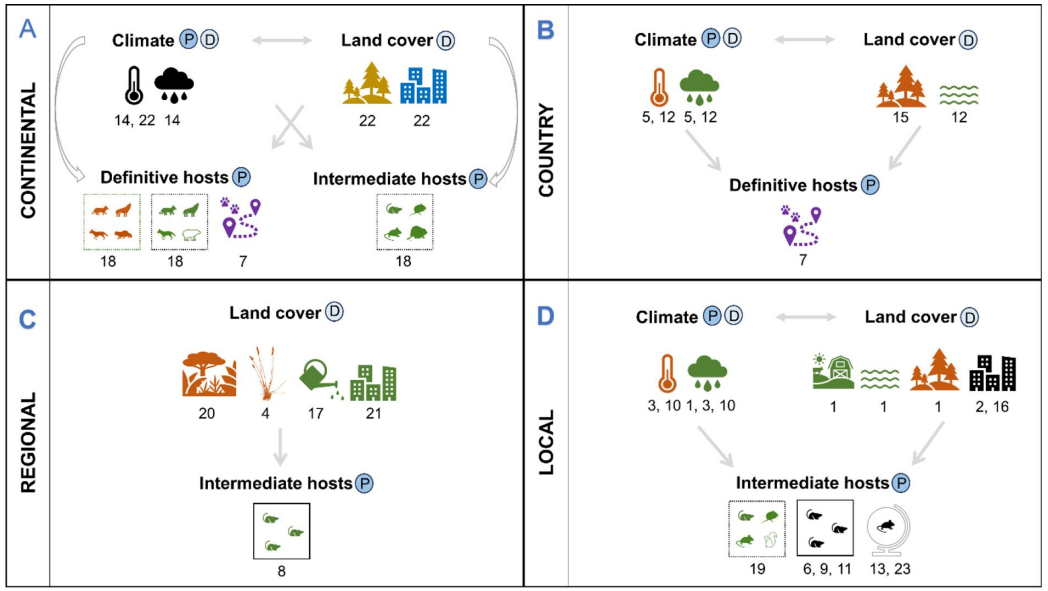
CONSISTENT ACROSS SCALES

Temperature negative · precipitation and humidity positive

Water bodies positive and forest cover negative, at both local and country scales

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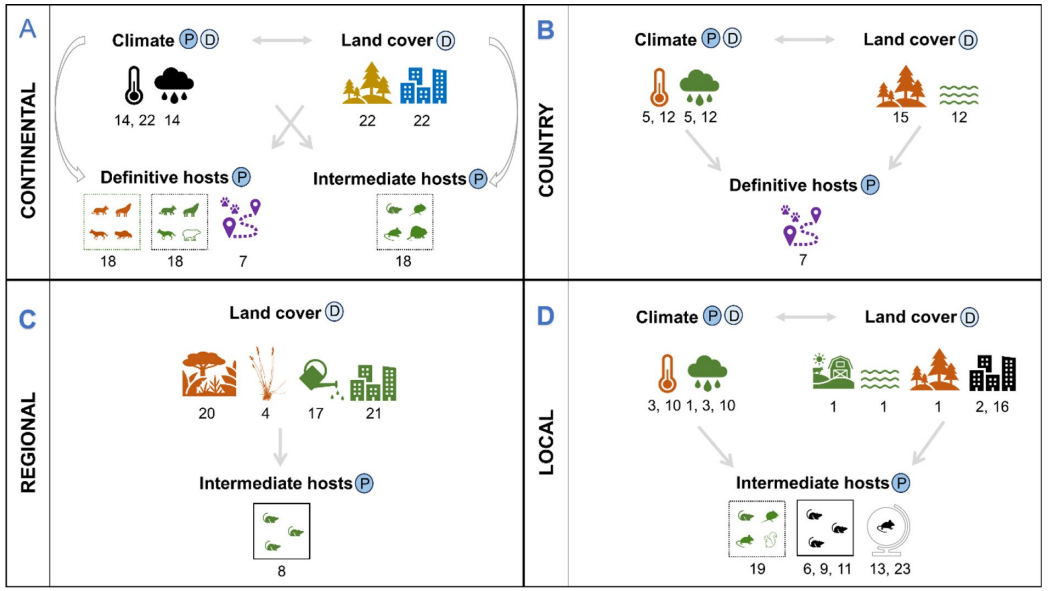
Continental: definitive-host dispersal, climate, intermediate-host ranges and host communities set range limits

Country/regional: the relative weight of climate vs land cover changes with the region

Local: carnivore functional responses to vole densities; defecation and marking sites create micro-foci

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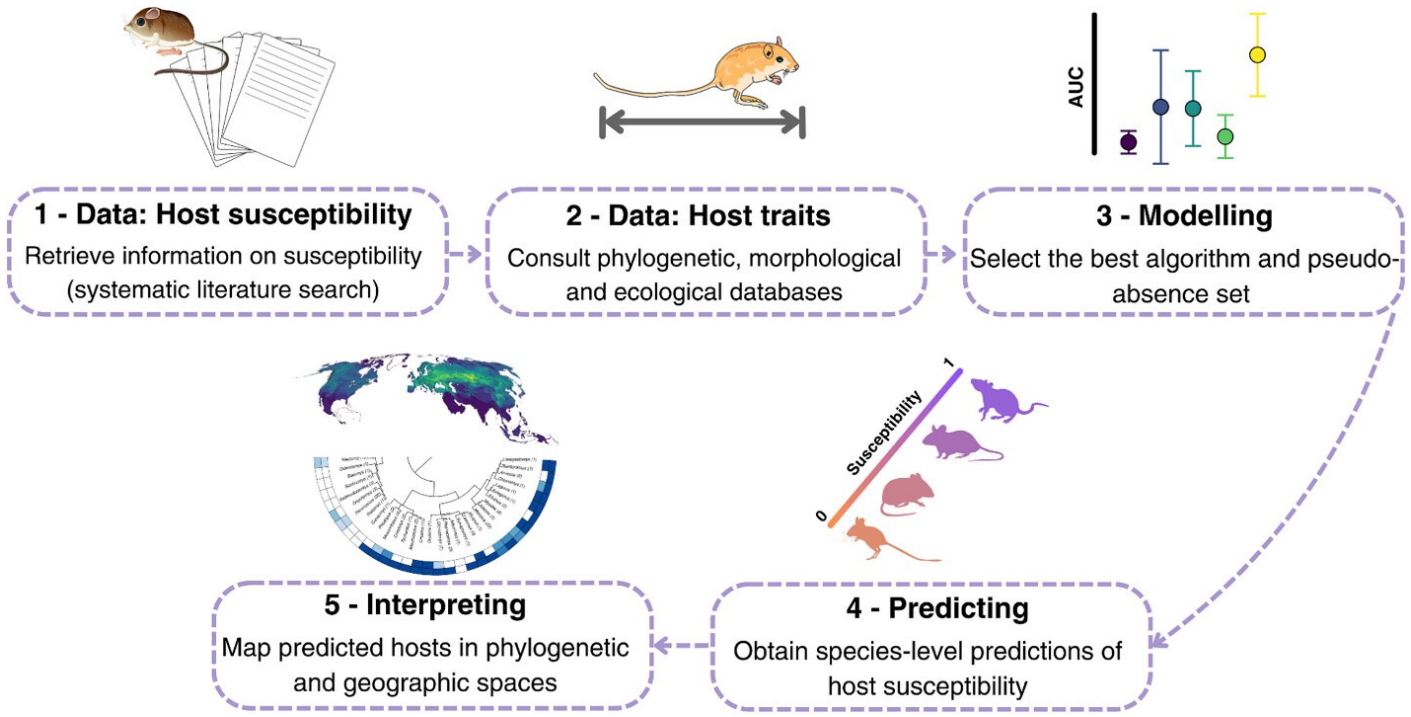
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NEXT STEP: COMPONENT-BASED MODELS THAT INCLUDE HOSTS

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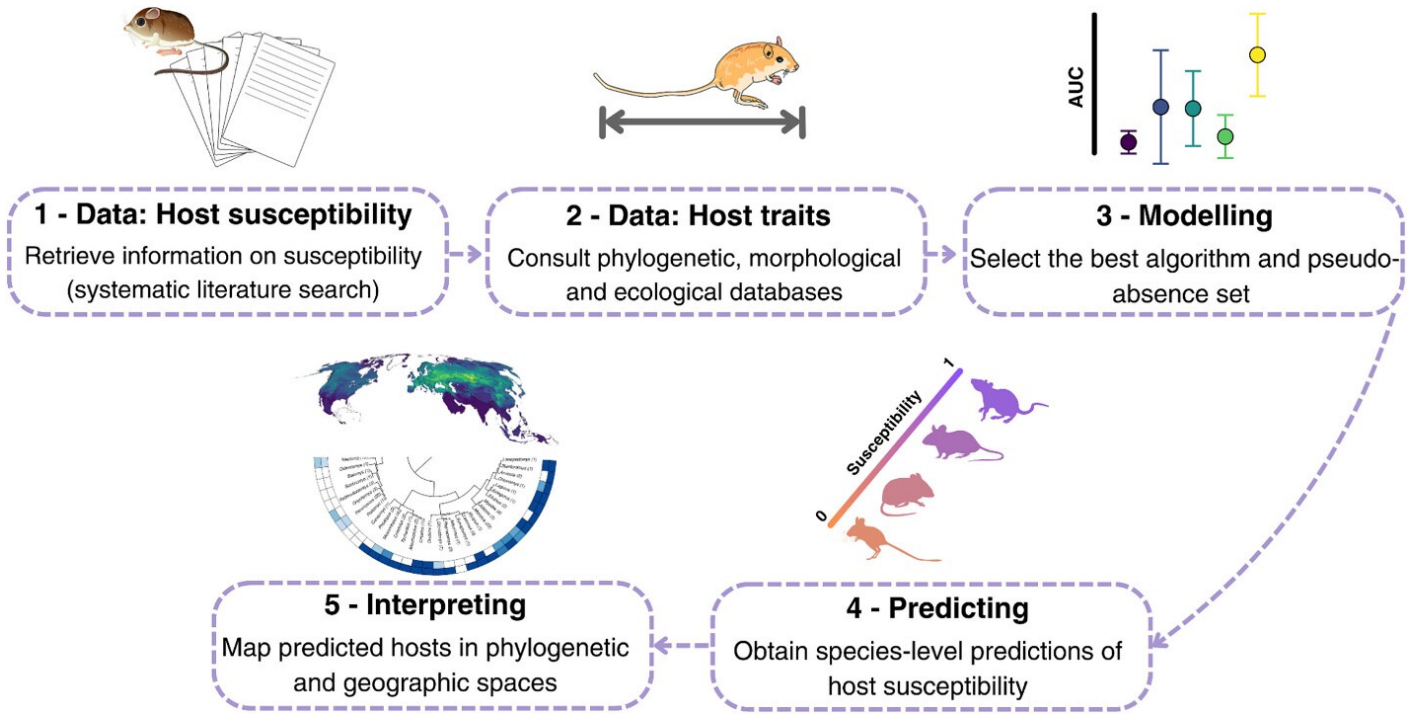
SIMONCINI ET AL. 2025 · HOSTS WITHOUT TRUE ABSENCES



Workflow: Simoncini et al. 2025, Ecol Inform (Fig. 1)

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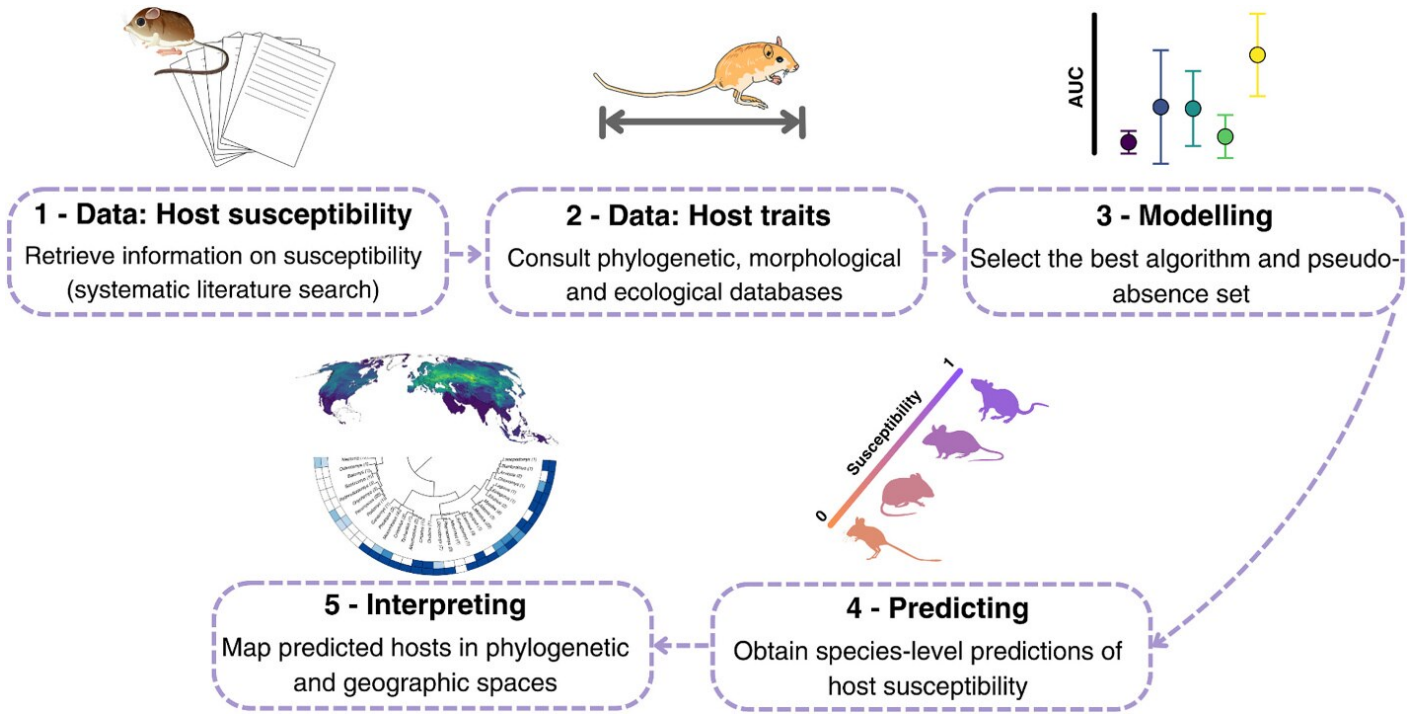
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THE PROBLEM

Positive records exist; reliable negatives (resistant species) almost never do

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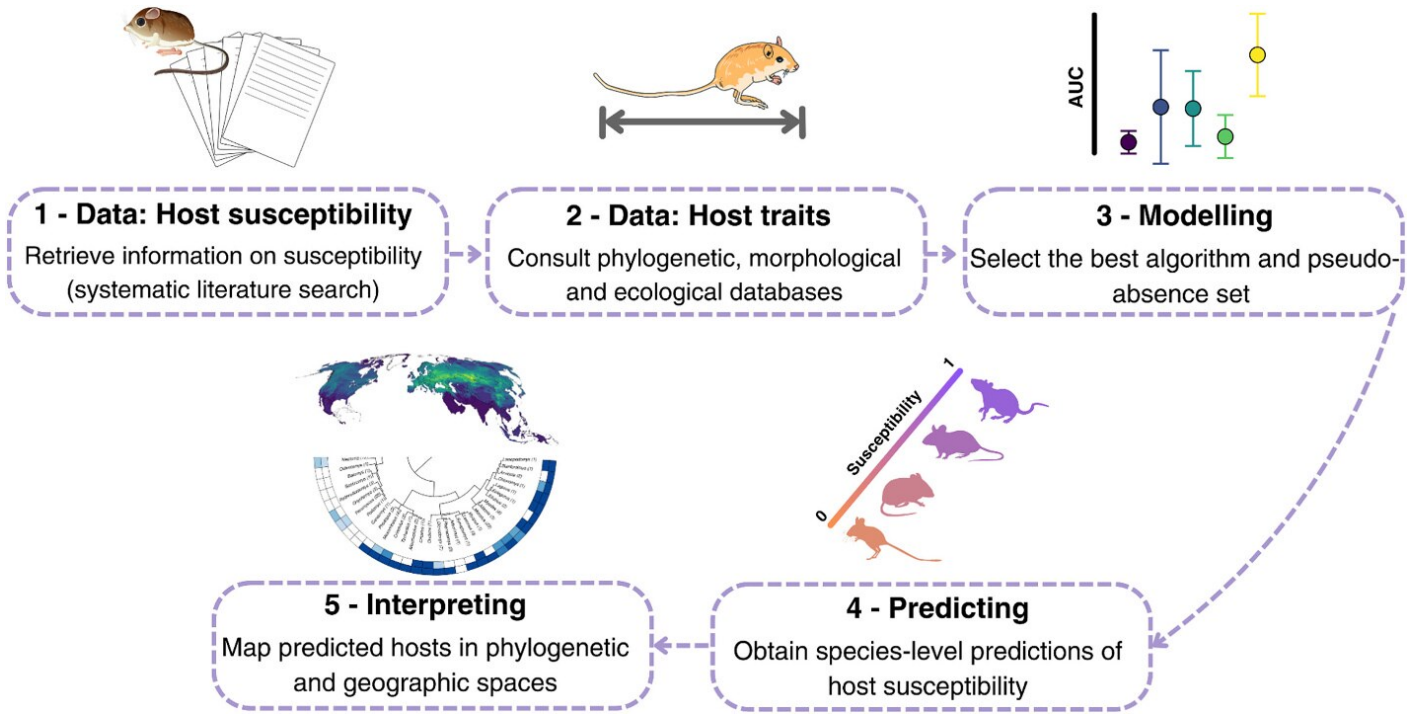
THE DATA

1,497 papers → 100 retained → infection status for 85 rodent species: 29 competent · 41 susceptible · 15 resistant

Simoncini et al. 2025, Ecol Inform (Methods; Results 3.1)

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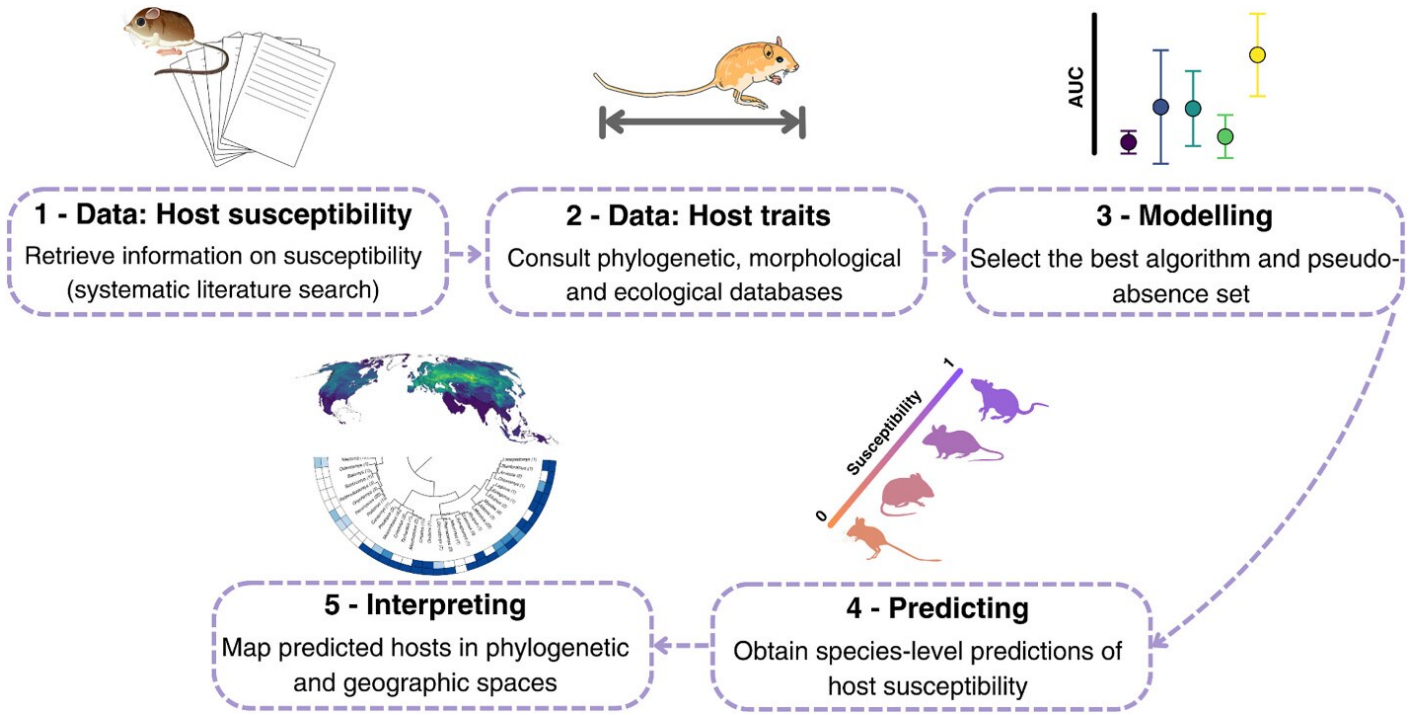
THE TRICK

Pseudo-absences drawn among unknown species with probability ∝ research effort (number of parasitological papers per species)

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SIMONCINI ET AL. 2025 · HOSTS WITHOUT TRUE ABSENCES



Workflow: Simoncini et al. 2025, Ecol Inform (Fig. 1)

Predictors: morphology, life history, range size, climate within the range · GLM vs presence–unlabelled learning · 100 pseudo-absence sets × 10-fold cross-validation · 587 Holarctic cricetid and murid rodents

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SIMONCINI ET AL. 2025 · WHO ARE THE MISSING HOSTS?

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SIMONCINI ET AL. 2025 · WHO ARE THE MISSING HOSTS?

BEST MODEL (GLM)

AUC 0.952 · TSS 0.857 · F1 0.897

GLM outperformed presence–unlabelled learning on all three metrics

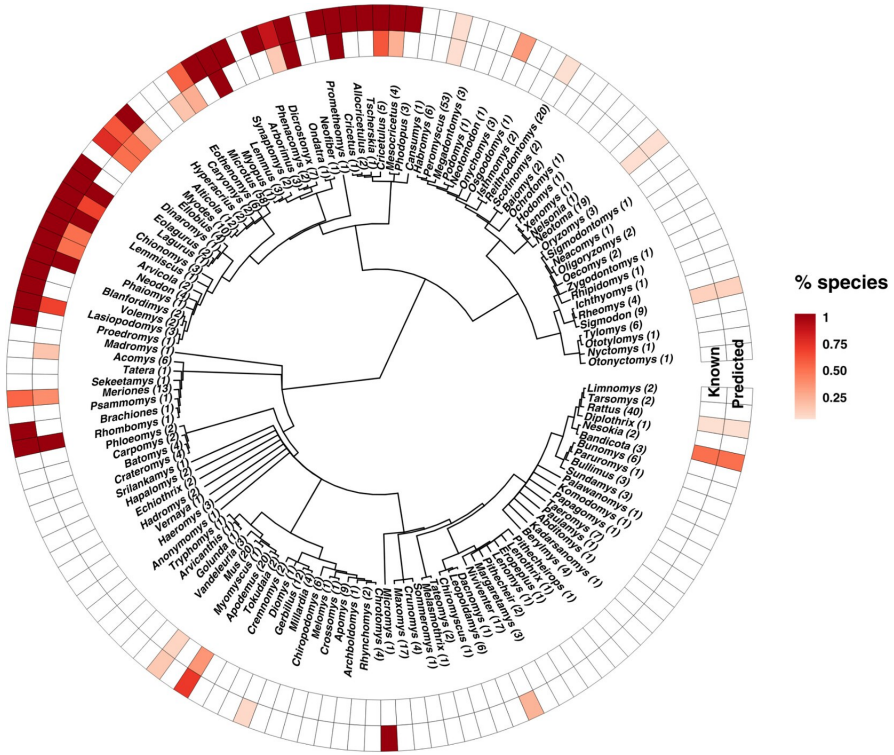
Mean temperature of the range $\beta = -1.49$, $z = -3.59$

Range size

$\beta = 0.70$, $z = 1.99$

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SIMONCINI ET AL. 2025 · WHO ARE THE MISSING HOSTS?



Proportion of species predicted susceptible per genus on the phylogeny: Simoncini et al. 2025 (Fig. 3)

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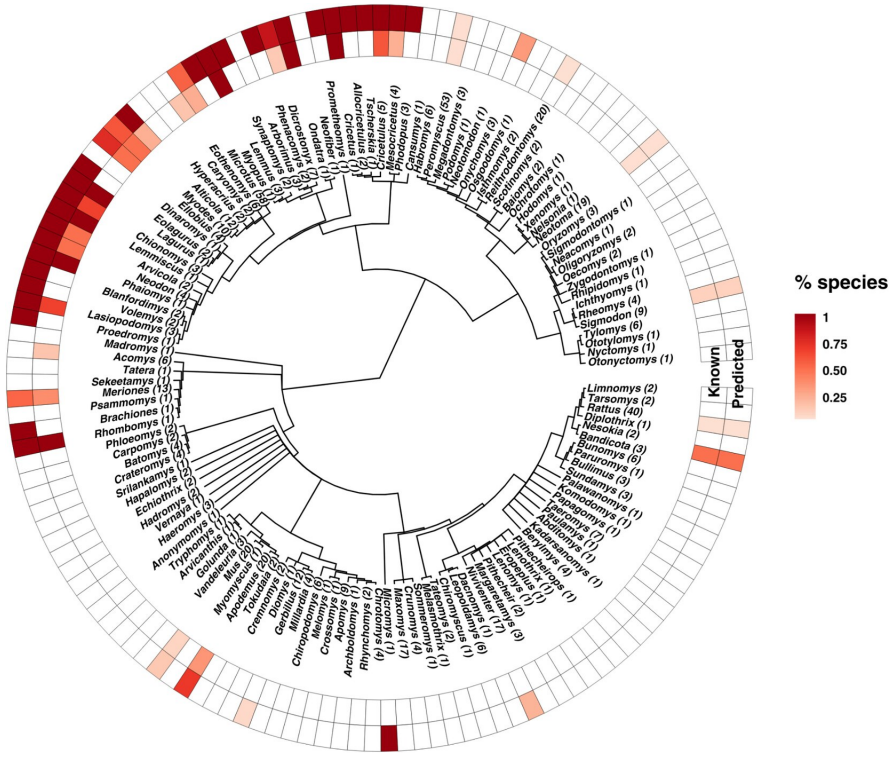
149 / 587

species predicted susceptible (25%)

Alticola 12/12 · Apodemus 14/20 · Microtus 32/58

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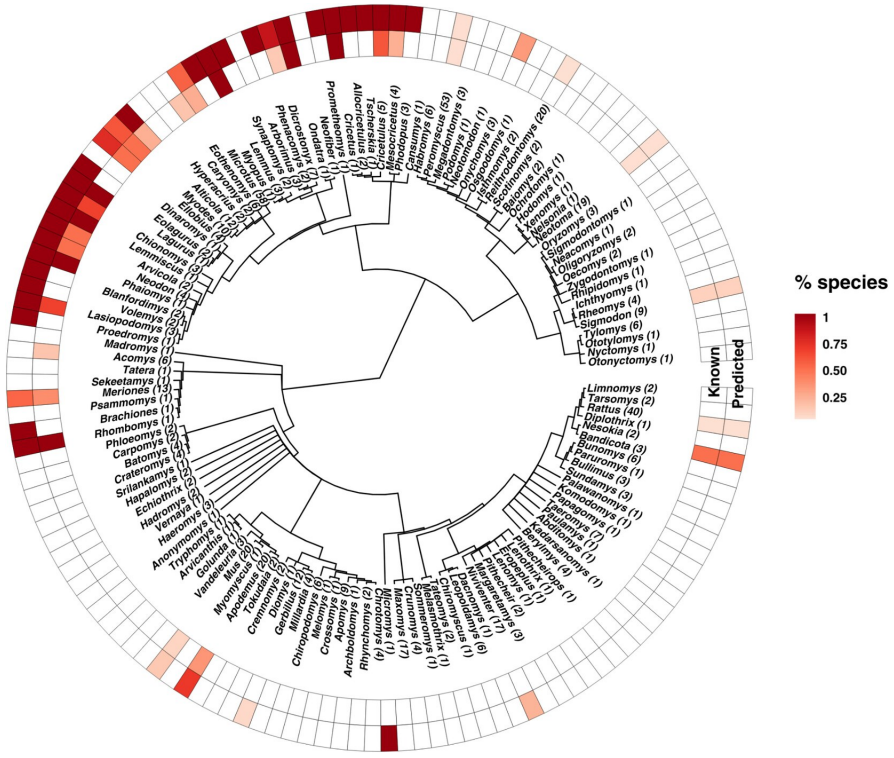
TOP PREDICTED, NEVER TESTED

Long-clawed mole vole *Prometheomys schaposchnikowi*	1.00
Taiga vole *Microtus xanthognathus*	0.98
Lemming vole *Alticola lemminus*	0.98
Northern collared lemming *Dicrostonyx groenlandicus*	0.97
Wood lemming *Myopus schisticolor*	0.96
Maximowicz's vole *Microtus maximowiczii*	0.94
Mongolian vole *Microtus mongolicus*	0.87

Selected from Table 1, Simoncini et al. 2025 (P = predicted probability of being a host)

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A SHORTLIST FOR TARGETED TRAPPING

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