Course contents:	1. Insect abundance and distribution: species-area relationships. Diversity of forest insects in relation to tree species, feeding guilds, and to the history of forest stands. Invasive species in forestry: definitions, concepts, and applications. 2. Classification of the outbreaks and related examples. Population dynamics: demographic growth versus mortality. Population cycles in different types of forest ecosystems. 3. Ecological factors affecting the populations of forest insects. Effects of climate and temperature, including climate change. Mechanisms of resistance developed by the host plants and adaptations of the insects. Role of competition and of natural enemies in population regulation. 4. Principles of integrated pest managements based on the knowledge of the insect ecology. Prevention, direct and indirect control, economic assessment of costs and benefits of IPM in forestry.

Outbreaks of forest insects and population dynamics

Insect Outbreaks Revisited

Edited by
Pedro Barbosa,
Deborah K. Letourneau
and Anurag A. Agrawal

WILEY-BLACKWELL

Outbreak types: gradients, cycles, eruptions

B. Zeiraphera diniana

Larch bud moth

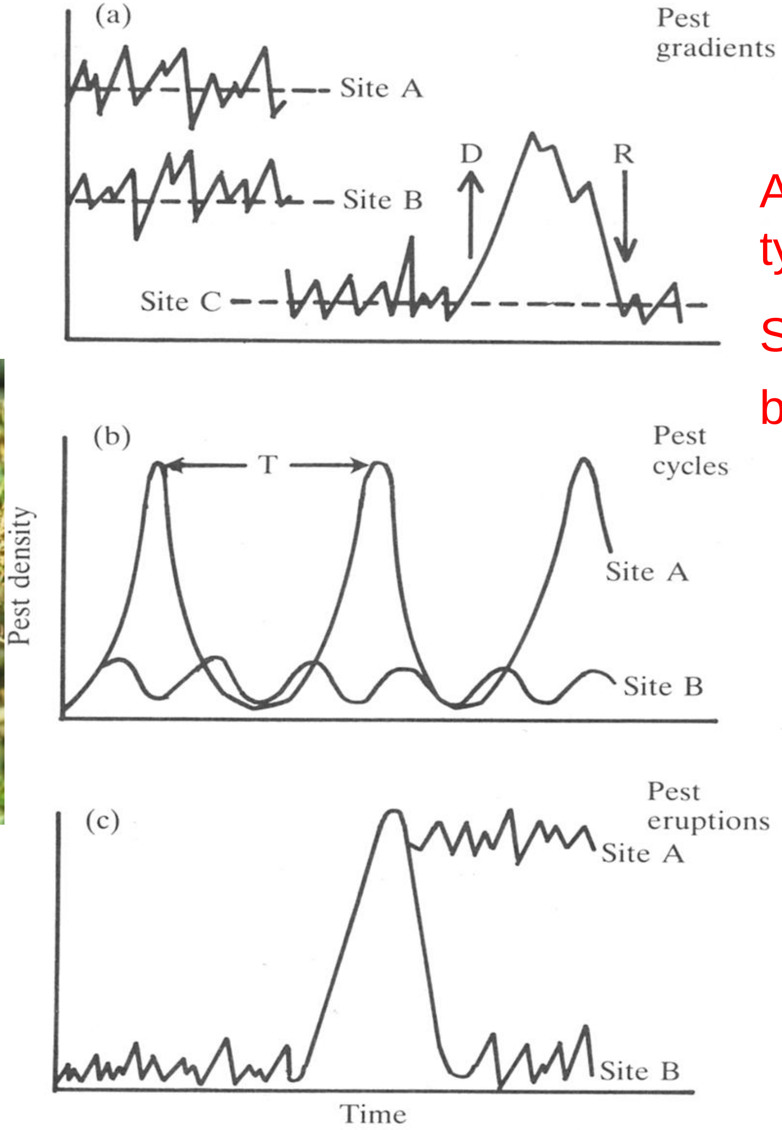


FIG. 1.2. Three major patterns of the population dynamics of forest insects (a) gradients (b) cycles, and (c) eruptions (D = disturbance in environmental conditions, R = return to normality, T = periodicity of population cycle) (see text) (from Berryman and Stark 1985).

A. Ips typographus

Spruce bark beetle

C. Cephalcia arvensis

Spruce web-spinning sawfly

Study of population dynamics

1. Construct a model of intergeneration change
2. Develop a sampling program and estimate number of individuals passing through each stage in life cycle
3. Construct a life table, calculate and interpret birth and death rates
4. Compare k-factor analysis as ways to discover factors causing population change
5. Distinguish major mortality factors, key factors
6. Distinguish direct density dependence, inverse density dependence, delayed density dependence, density independence
7. Critically evaluate methods for assessing role of density-dependent and density-independent factors in population dynamics

Classical Approach: Key Factor Analysis

1. Study life history and develop methods of census for each stage
2. Construct a life table that is as complete as possible
3. Accumulate many life tables
4. Plot generation curves and mortalities
5. Assess the key-factors which make the biggest contribution to change in generation mortality
6. Determine the relationship of component mortalities to density
7. Follow up with intensive studies of key factors
8. Make predictions using the model

Study life history and develop methods of census for each stage

1. Life History
   - Adult emergence
   - Oviposition
   - Larvae and Pupae

2. Sampling decisions
   - Subdivision of the habitat
   - Selection of the sampling unit
   - Number of samples
   - Placement of samples
   - Timing of sampling

Construct a life table that is as complete as possible

1. Designate stage intervals – how?
2. Estimate mortality assuming factors act sequentially, not simultaneously – what are the implications?
3. Estimate k-values as difference between logarithms of the population before and after mortality acts

Concept Alert!

- Major mortality factor – makes a large contribution to mortality within a generation (large *k*)
- Key factors contribute to changes in abundance between generations (component *k* most correlated with generation K_{total})
- Density-regulating factors are those *k*-values that increase with density of the stage on which they act.
- Population regulation. A regulated population is one that tends to return to equilibrium density or cycle when perturbed from this level or cycle. Precise DD requires that DD factors not be too strong or too weak.

Test for density dependence: plot k values against density

1. Strength

2. Sign

3. Time Delay

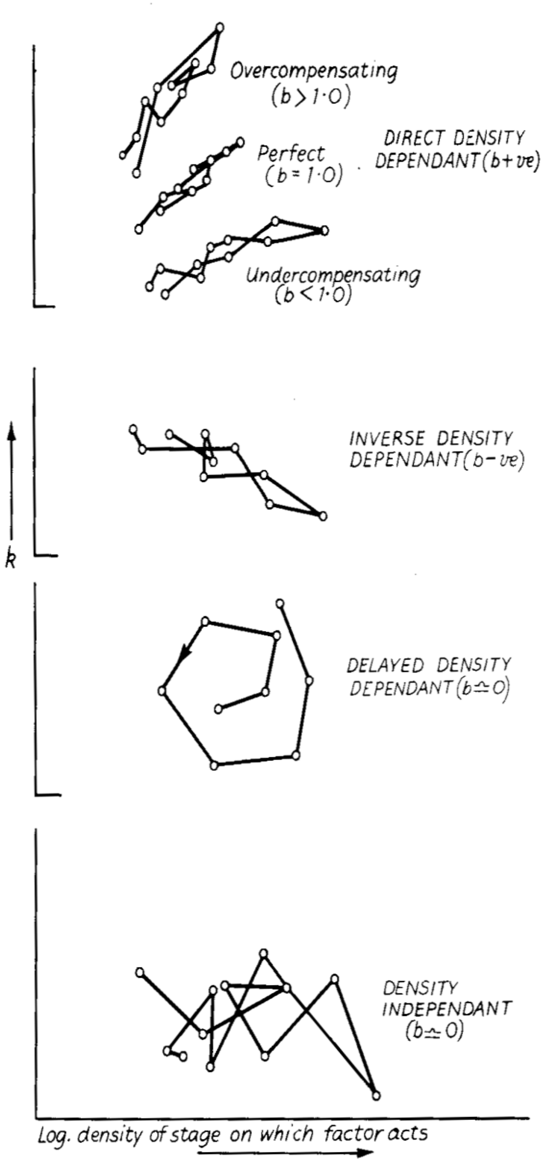


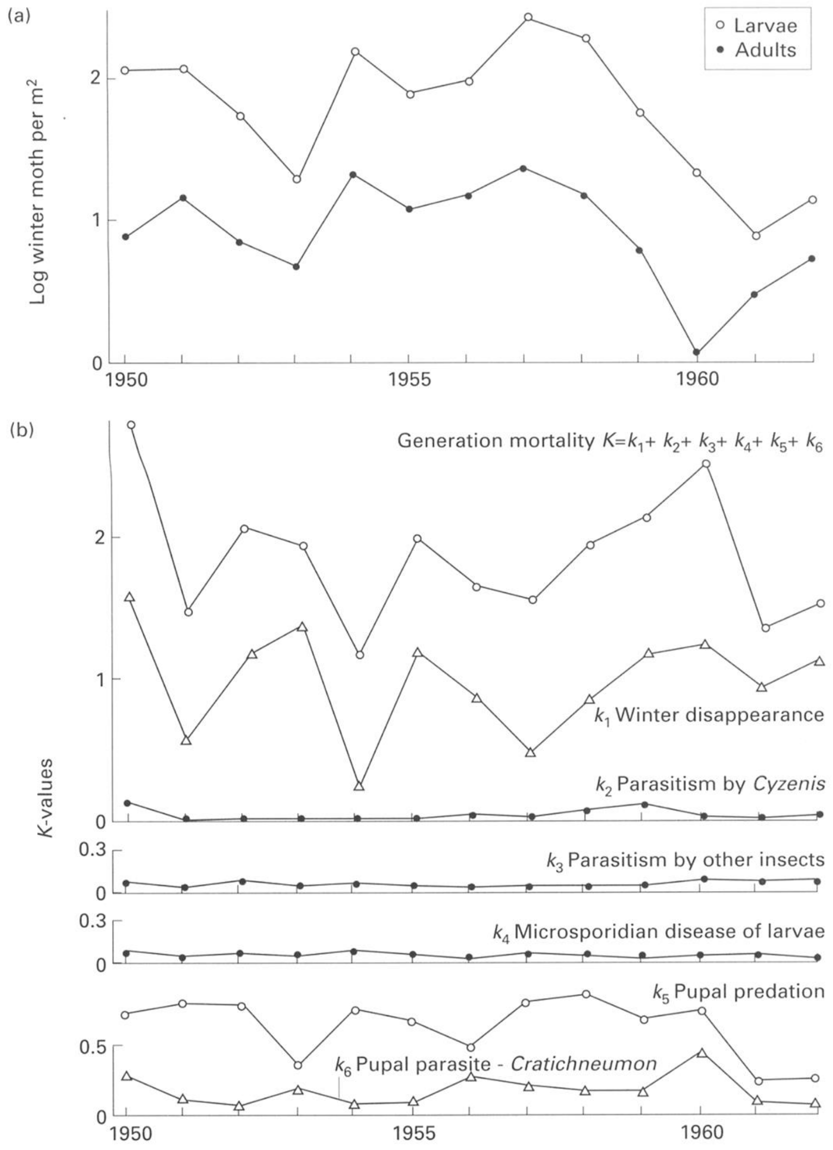
Fig. 10.7 Time sequence plots showing how the different density relationships may be recognized from the patterns produced.

Case study
Winter Moth
Operophtera brumata
Geometridae

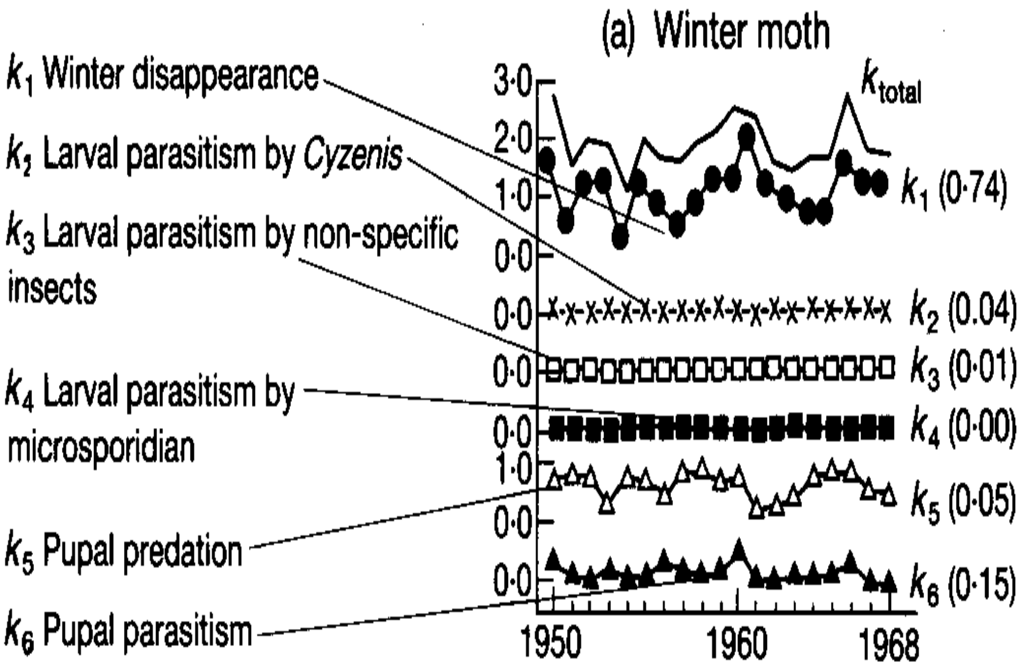
Operophtera brumata
the winter moth

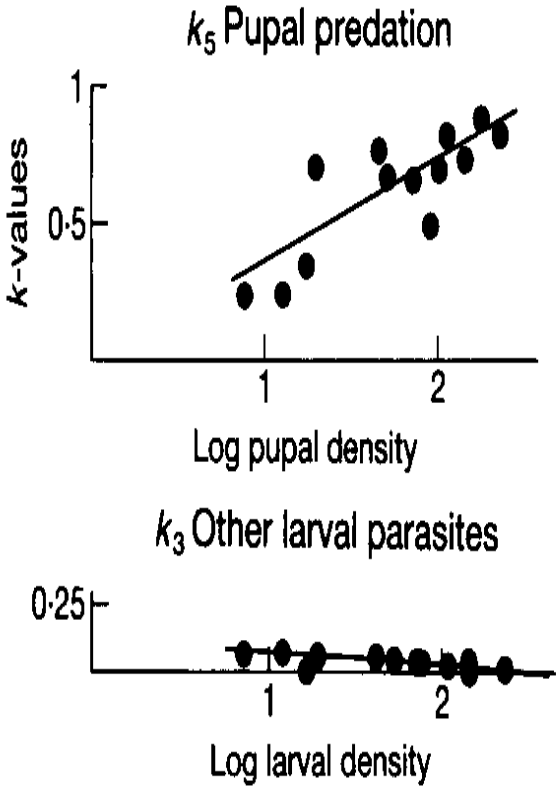
- Univoltine -one generation per year
- Female flightless
- Cyclic dynamics: 9-10 years between population peaks. Parasitoids important factor for cycles.
- Main host species: *Quercus robur*- Pedunculate Oak native to large parts of Europe. Birch- *Betula* sp. in northern Europe.
- Other host tree species: mountain ash, fruit trees (mostly Rosacea) and other.

Winter moth life table of Varley and Gradwell 1970



Plot k against time and density





Plot k against time and density: delayed dd and anti-clockwise direction

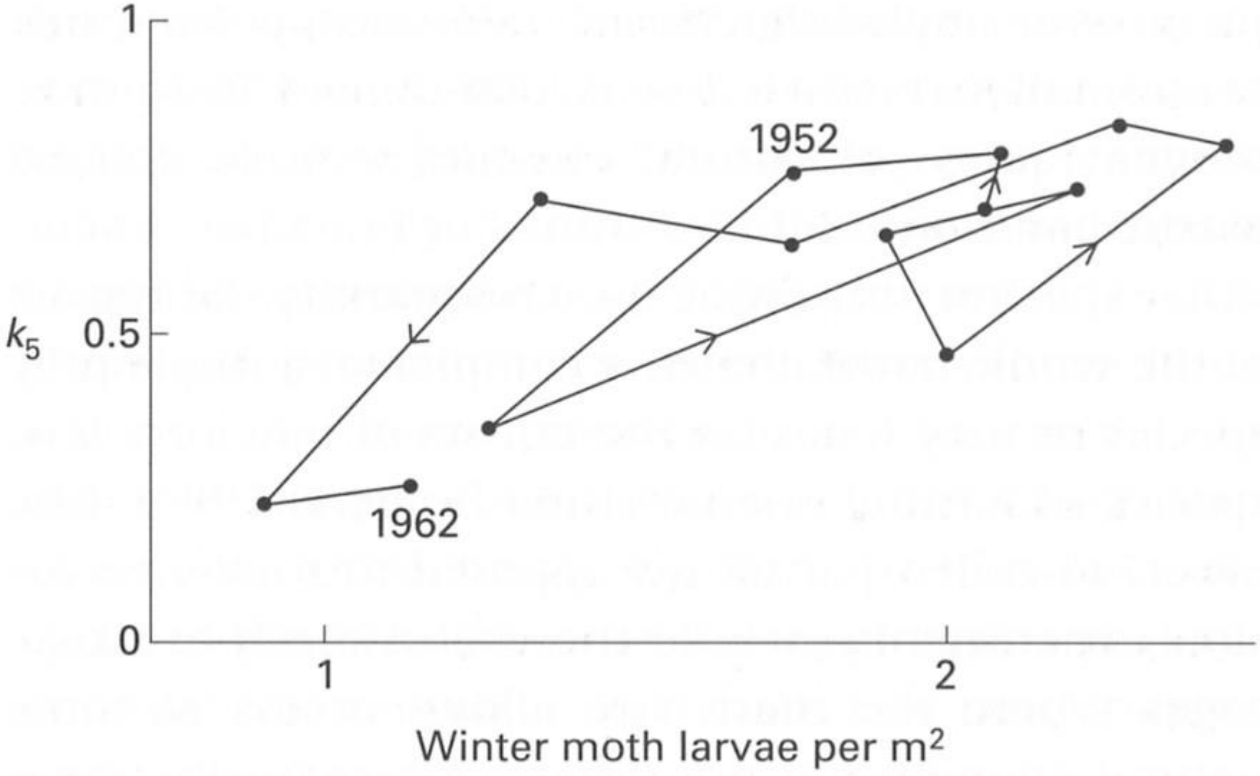


Fig. 5.14 Time series plot of pupal predation of the winter moth, the spiral form suggesting a delayed density-dependent component to this mortality. (Source as Fig. 5.12.)

The special case of population cycles

- Larch bud moth *Zeiraphera diniana*
- Gypsy moth *Lymantria dispar*
- Winter moth *Operophtera brumata*

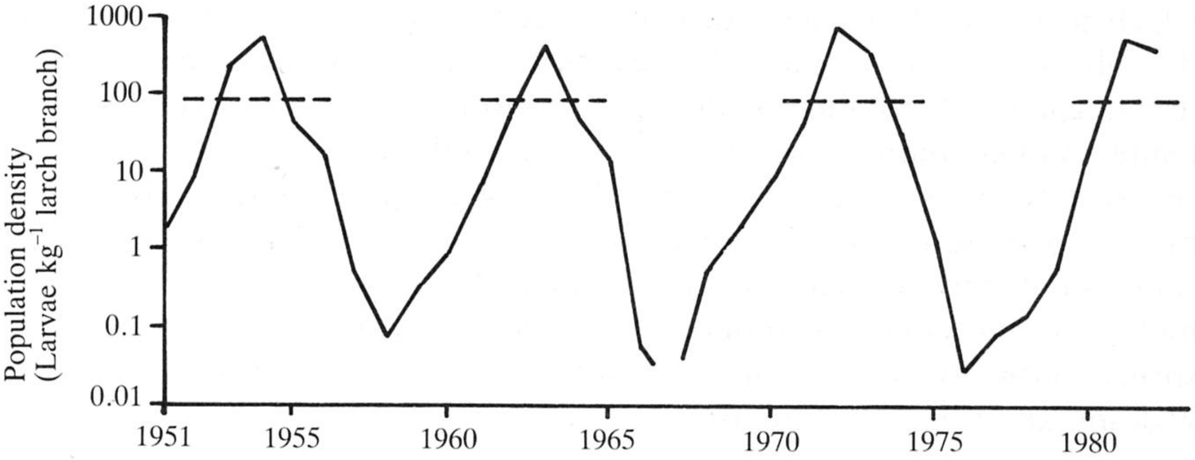


FIG. 1.3. Fluctuation in numbers of larvae of *Zeiraphera diniana* on larch at Sils in the Engadine Valley, Switzerland. Dotted line is the defoliation threshold (from Baltensweiler 1984).

Larch bud moth

Zeiraphera diniana

Engadine, Switzerland

Special Edition: Obituary Werner Baltensweiler, 1926-2008

Werner Baltensweiler measuring larch needle length near Zuoz, Switzerland, September, 2002

Ecology, 84(5), 2003, pp. 1207–1214

DYNAMICAL EFFECTS OF PLANT QUALITY AND PARASITISM ON POPULATION CYCLES OF LARCH BUDMOTH

Peter Turchin,[1] Simon N. Wood,[2] Stephen P. Ellner,[3] Bruce E. Kendall,[4] William W. Murdoch,[5]
Andreas Fischlin,[6] Jérome Casas,[7] Edward McCauley,[8] and Cheryl J. Briggs[9]

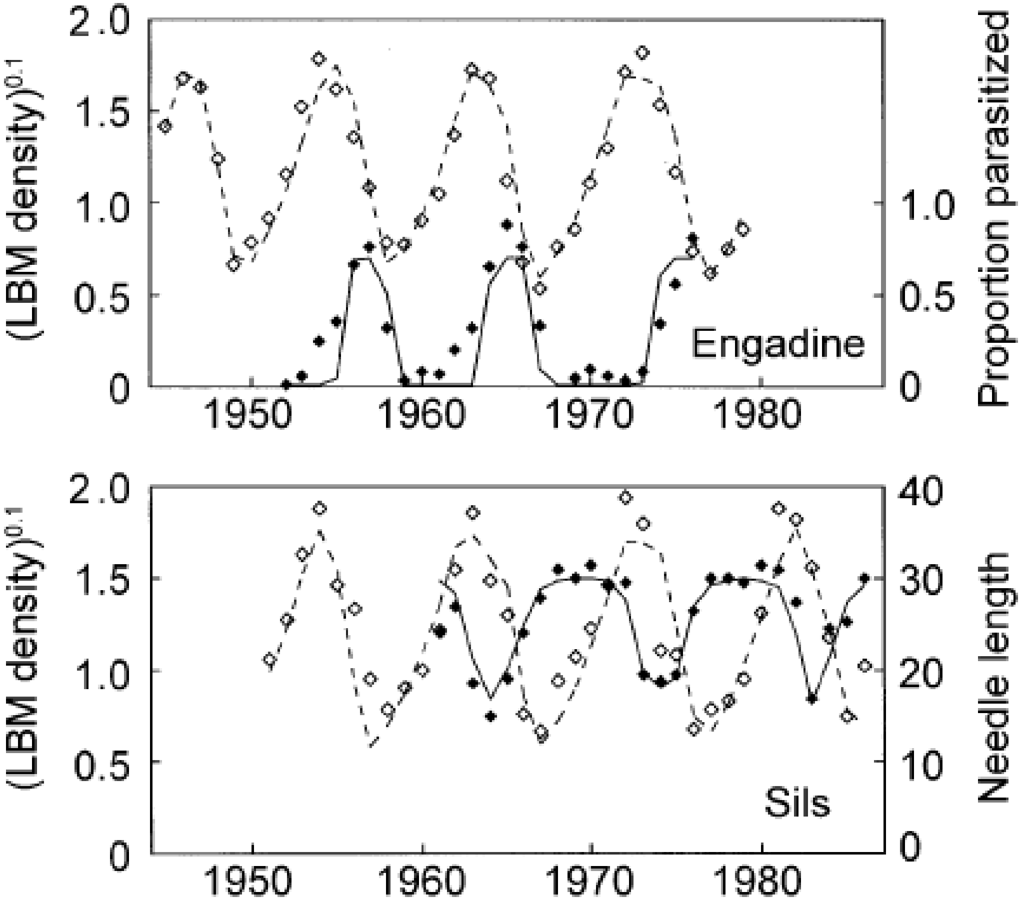


FIG. 3. Results of trajectory matching. Upper panel: Engadine data set (hollow symbols indicate budmoth density; filled symbols indicate proportion parasitized). Lower panel: Sils data set (hollow symbols indicate budmoth density; filled symbols indicate needle length).

Ecology, 91(1), 2010, pp. 106–118

Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling

OTTAR N. BJØRNSTAD,[1,4] CHRISTELLE ROBINET,[2,3] AND ANDREW M. LIEBHOLD[3]

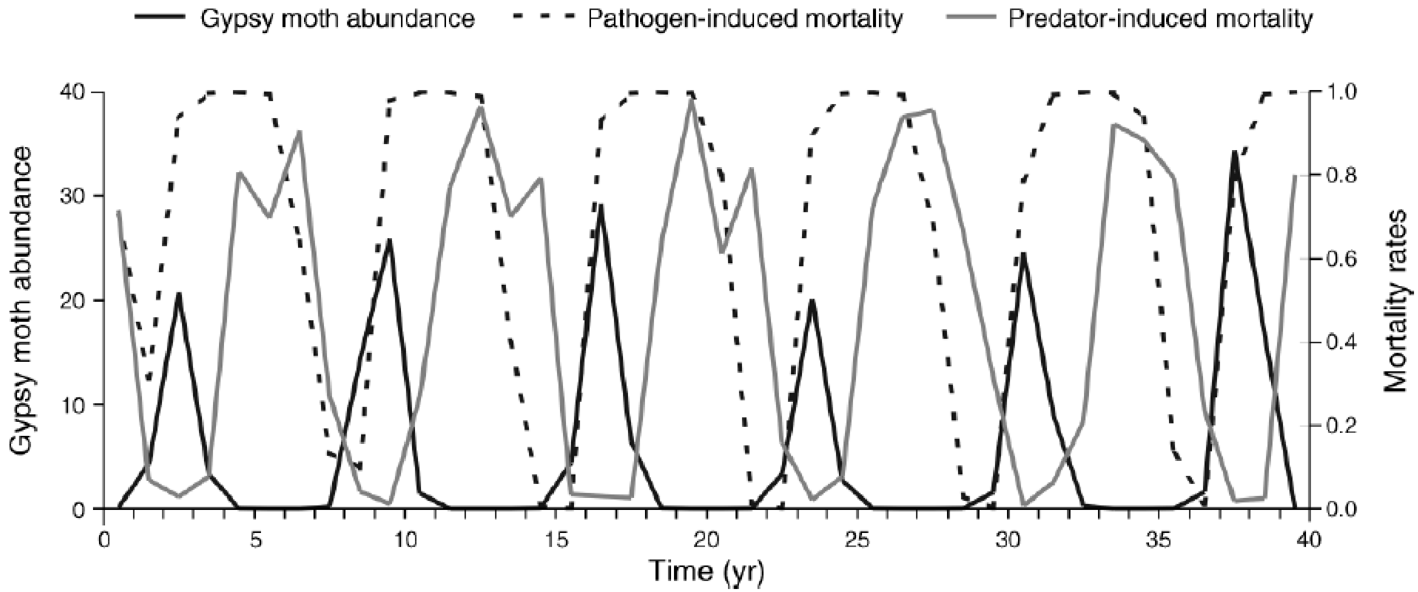


FIG. 2. An example of fluctuations of gypsy moth abundance (in arbitrary units) predicted by the stochastic model with associated mortality rates due to predators and pathogens when predator carrying capacity $K = 5$, and predator growth rate is log-normal with r (the mean instantaneous rate of increase) $= 2$ and $\tilde{\sigma} = 0.3$).

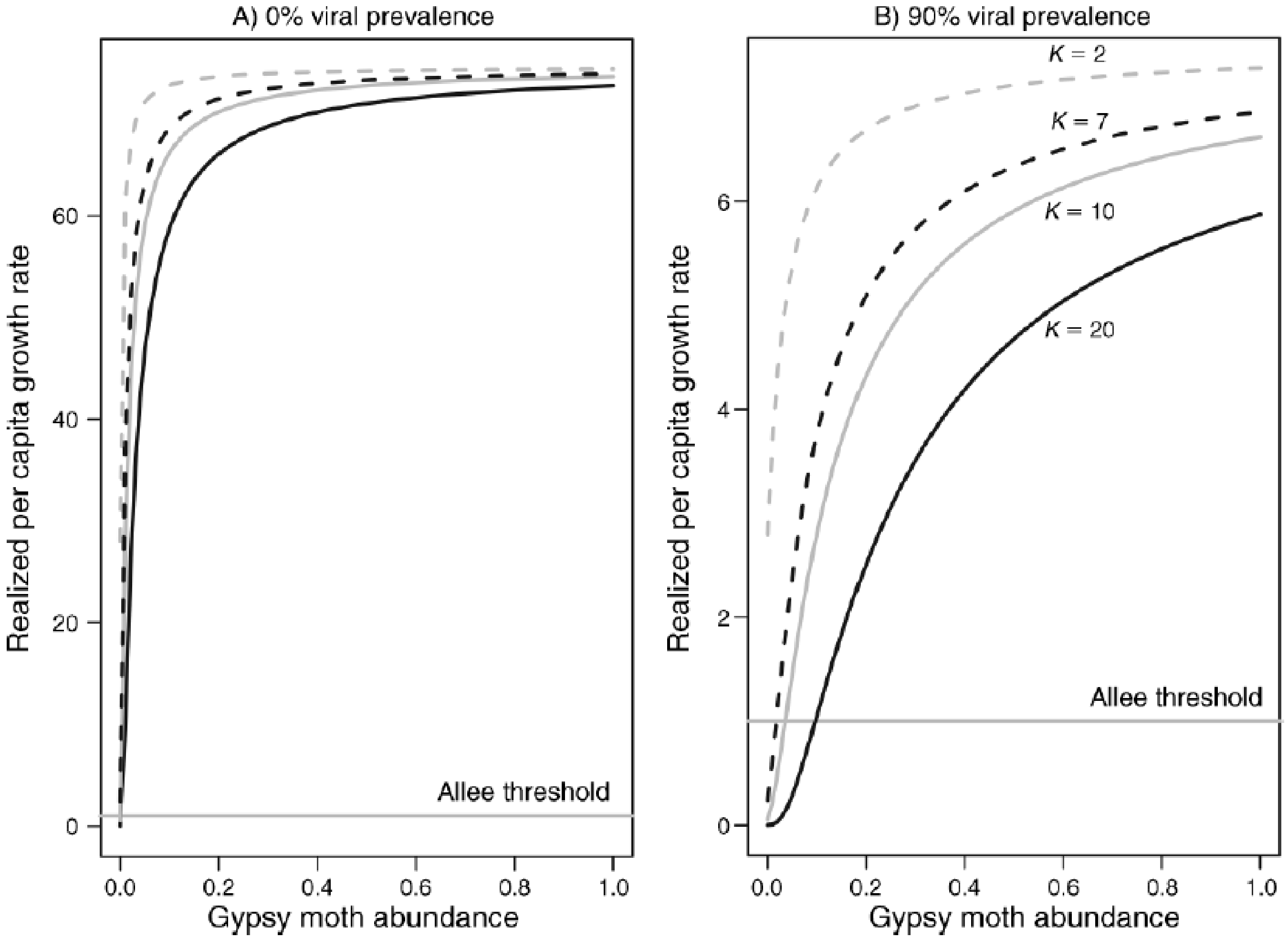
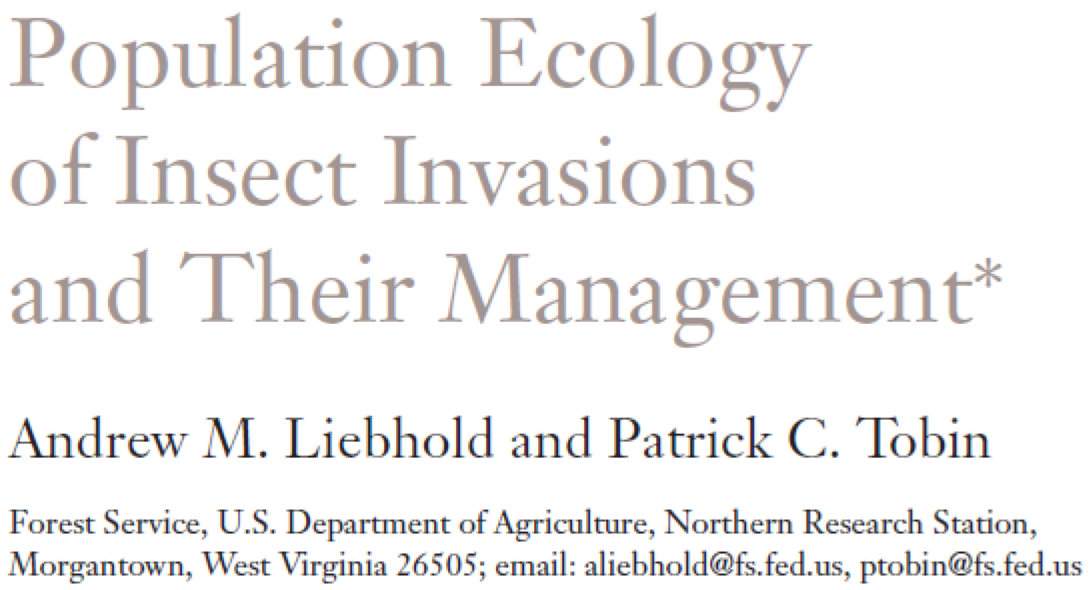


FIG. 3. Effects of predator abundance on low-density populations of gypsy moth, when (A) no host is infected with virus, and when (B) 90% of larvae are infected with virus. The solid black line refers to K (carrying capacity) $= 20$, the solid gray line refers to $K = 10$, the dashed black line refers to $K = 7$, and the dashed gray line refers to $K = 2$. The horizontal gray line indicates a realized per capita growth rate of 1 (the Allee threshold).



Population Ecology of Insect Invasions and Their Management*

Andrew M. Liebhold and Patrick C. Tobin

Forest Service, U.S. Department of Agriculture, Northern Research Station,
Morgantown, West Virginia 26505; email: aliebhold@fs.fed.us, ptobin@fs.fed.us

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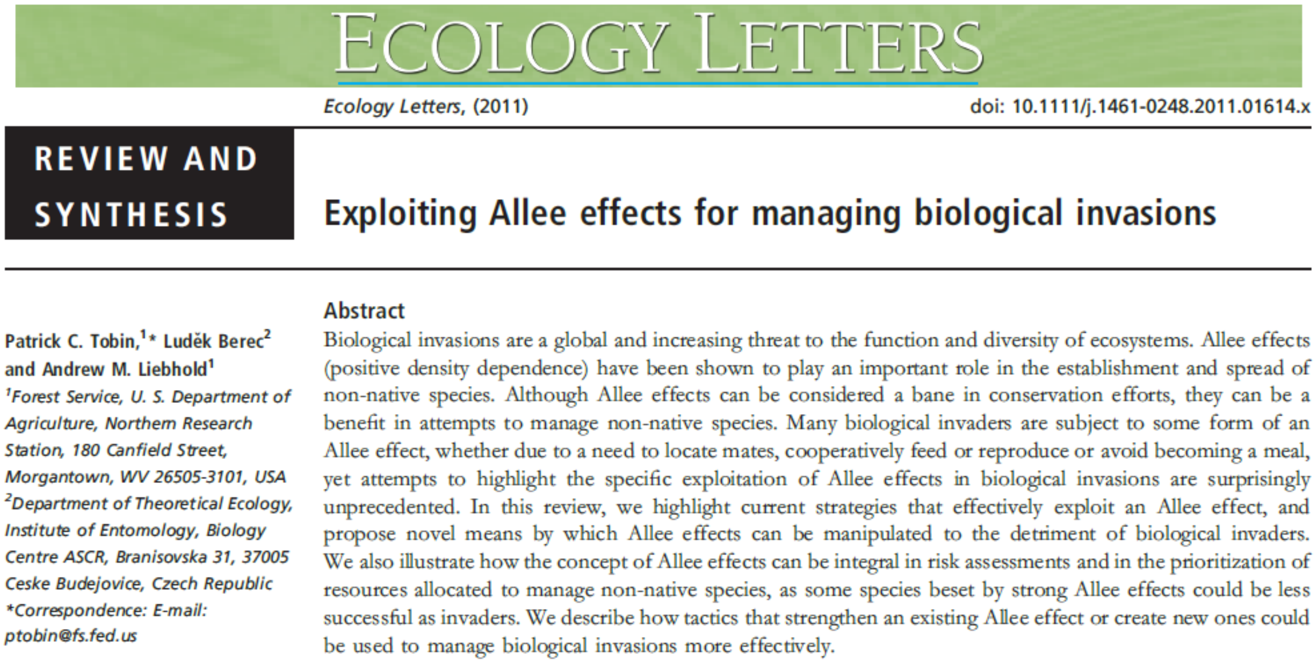

ECOLOGY LETTERS

Ecology Letters, (2011) doi: 10.1111/j.1461-0248.2011.01614.x

REVIEW AND SYNTHESIS

Exploiting Allee effects for managing biological invasions

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Abstract

Biological invasions are a global and increasing threat to the function and diversity of ecosystems. Allee effects (positive density dependence) have been shown to play an important role in the establishment and spread of non-native species. Although Allee effects can be considered a bane in conservation efforts, they can be a benefit in attempts to manage non-native species. Many biological invaders are subject to some form of an Allee effect, whether due to a need to locate mates, cooperatively feed or reproduce or avoid becoming a meal, yet attempts to highlight the specific exploitation of Allee effects in biological invasions are surprisingly unprecedented. In this review, we highlight current strategies that effectively exploit an Allee effect, and propose novel means by which Allee effects can be manipulated to the detriment of biological invaders. We also illustrate how the concept of Allee effects can be integral in risk assessments and in the prioritization of resources allocated to manage non-native species, as some species beset by strong Allee effects could be less successful as invaders. We describe how tactics that strengthen an existing Allee effect or create new ones could be used to manage biological invasions more effectively.

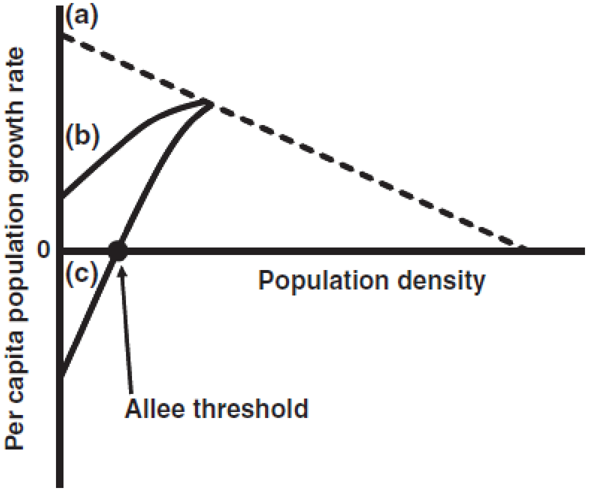


Figure 1 Representation of the change in the per capita population growth rate over increasing population density. (a) Classic negative density dependence. (b) Weak Allee effect in which the population growth rate declines at low densities but remains positive. (c) Strong Allee effect in which the population growth rate is negative at low densities. The Allee threshold is thus the minimum population size to ensure persistence (modified from Taylor & Hastings 2005).

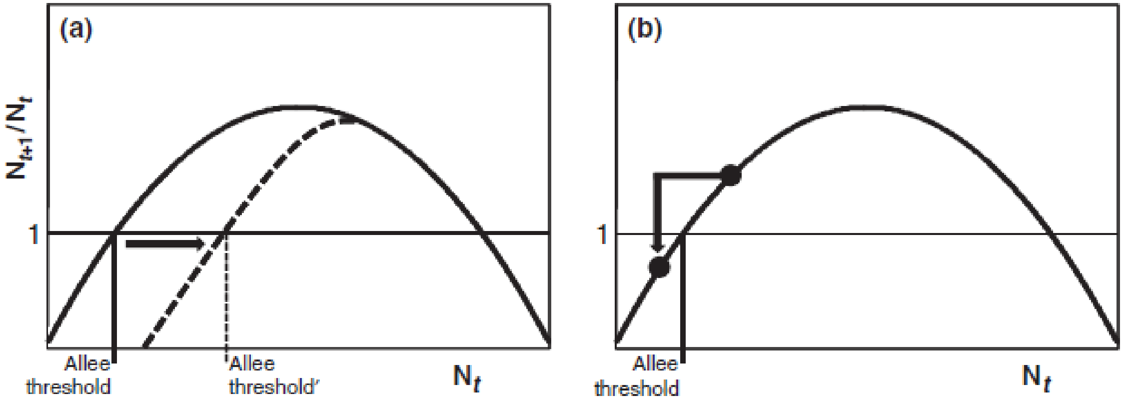
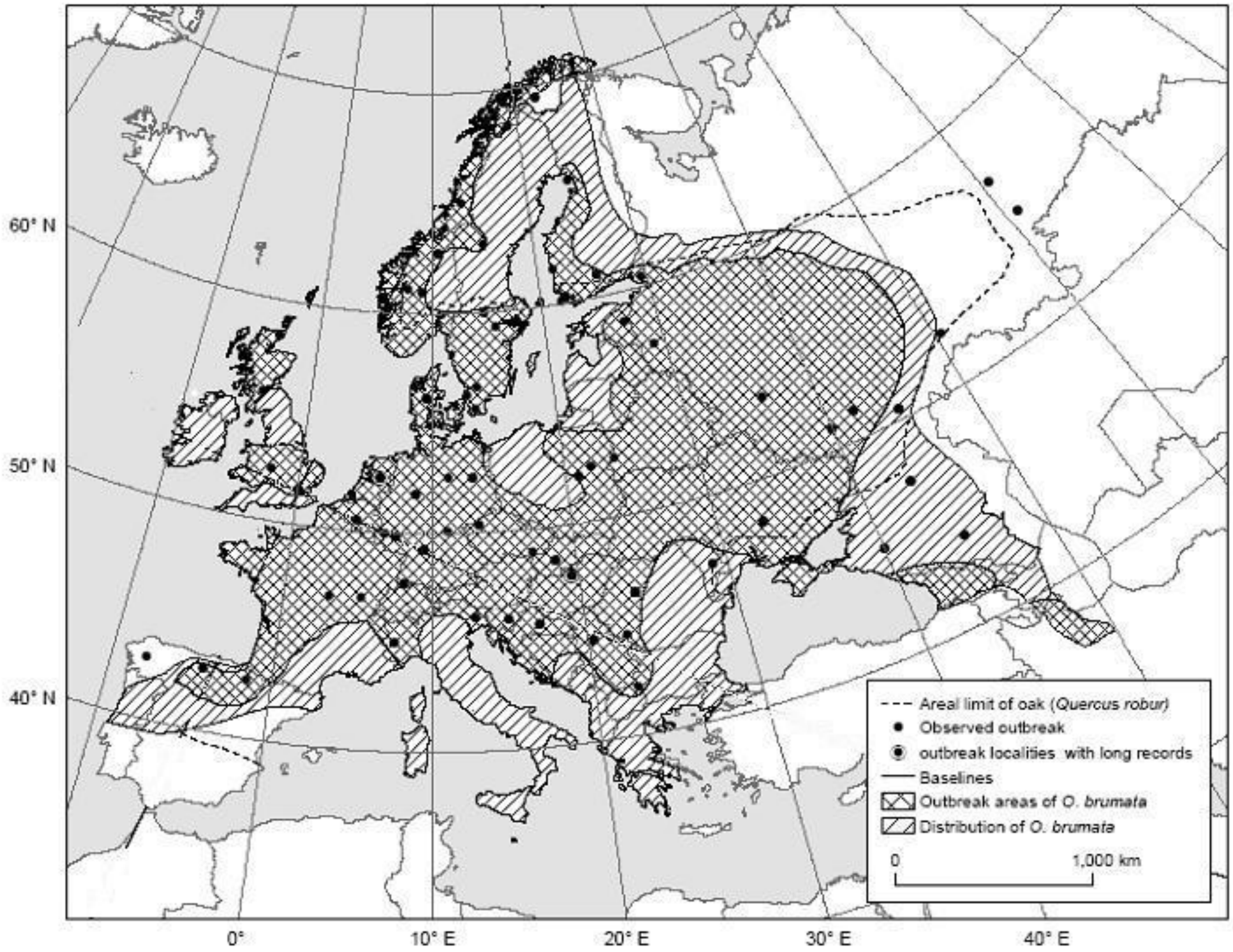


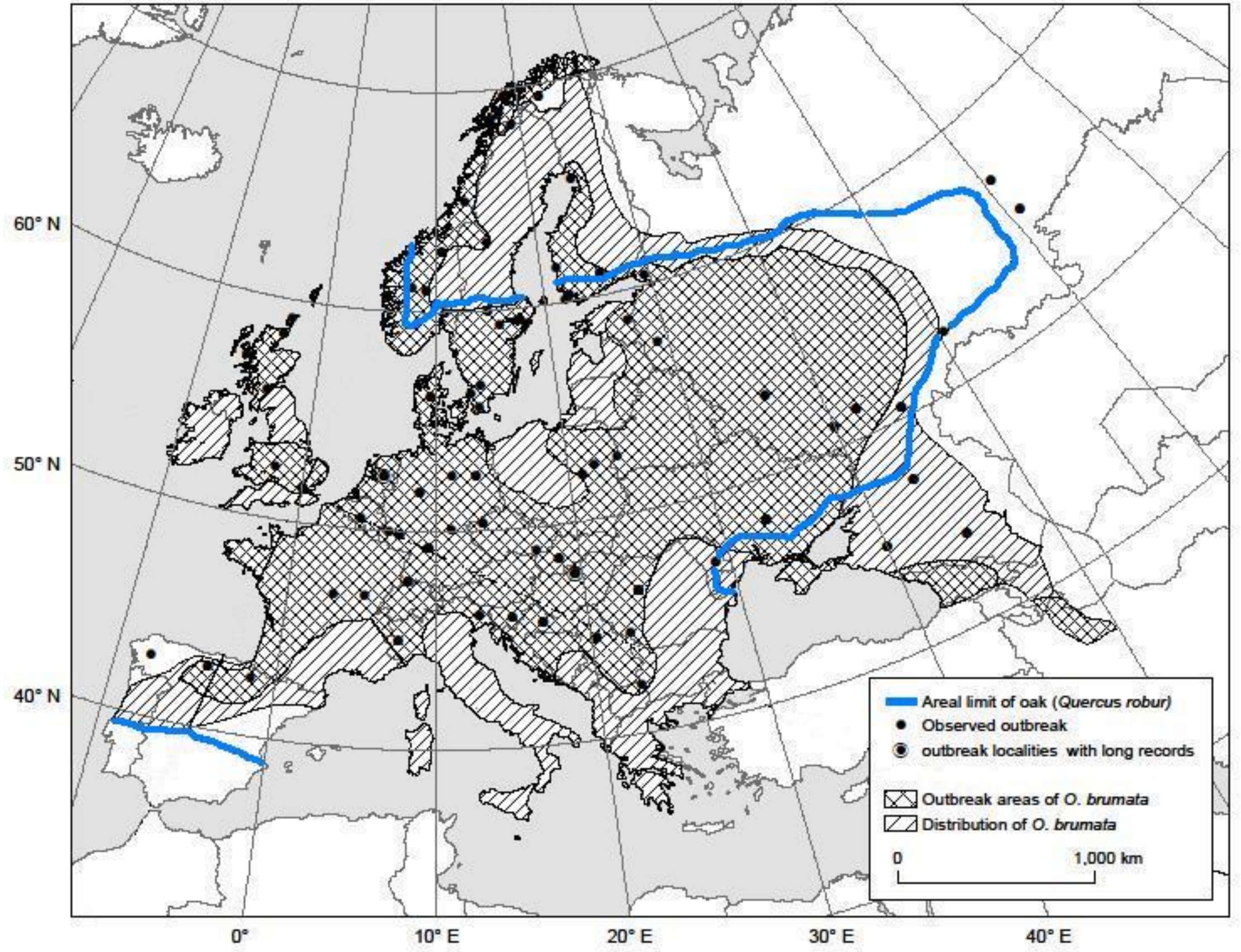
Figure 2 Exploiting an Allee effect in population management. The change in population density, N_{t+1}/N_t is plotted as a function of density at the beginning of the generation, N_t. (a) Strategies such as mating disruption, which do not directly affect population density, can strengthen an existing Allee effect due to mate-finding failure; thus, a higher density N_t is required to surpass the modified Allee threshold′. (b) Removing individuals from a population may not affect the Allee threshold as in (a), but it could still lead to population decline even if not all individuals are killed. Some tactics, such as mass trapping, or a combination of tactics, could effectively accomplish both (a) and (b) (modified from Liebhold & Tobin 2008).

Winter moth defoliation at Lapporten-Lappland Photo S. Hörnell

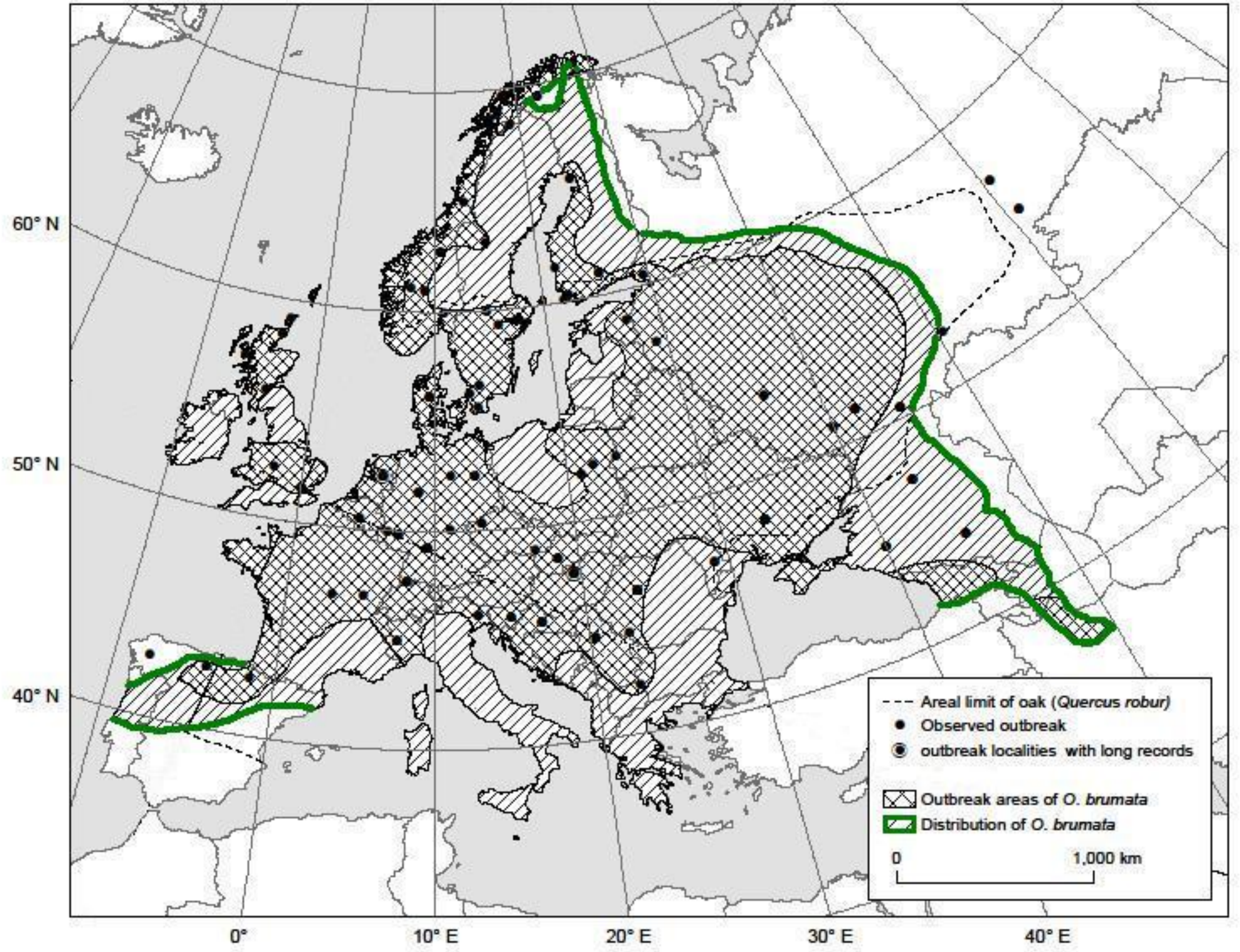
Reported Outbreak localities 1948-2008



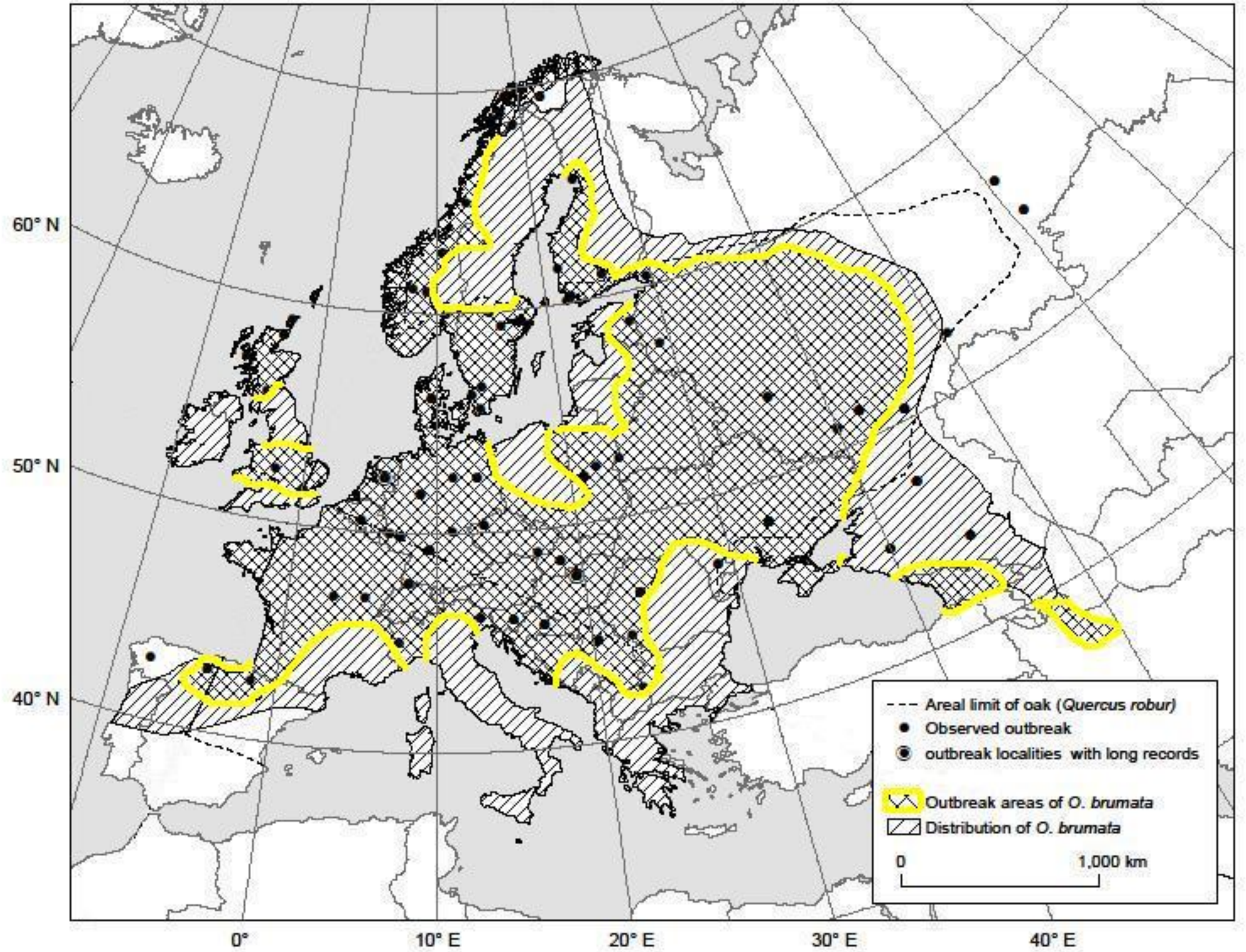
Oak distribution range



Distribution range of *Operophtera brumata*

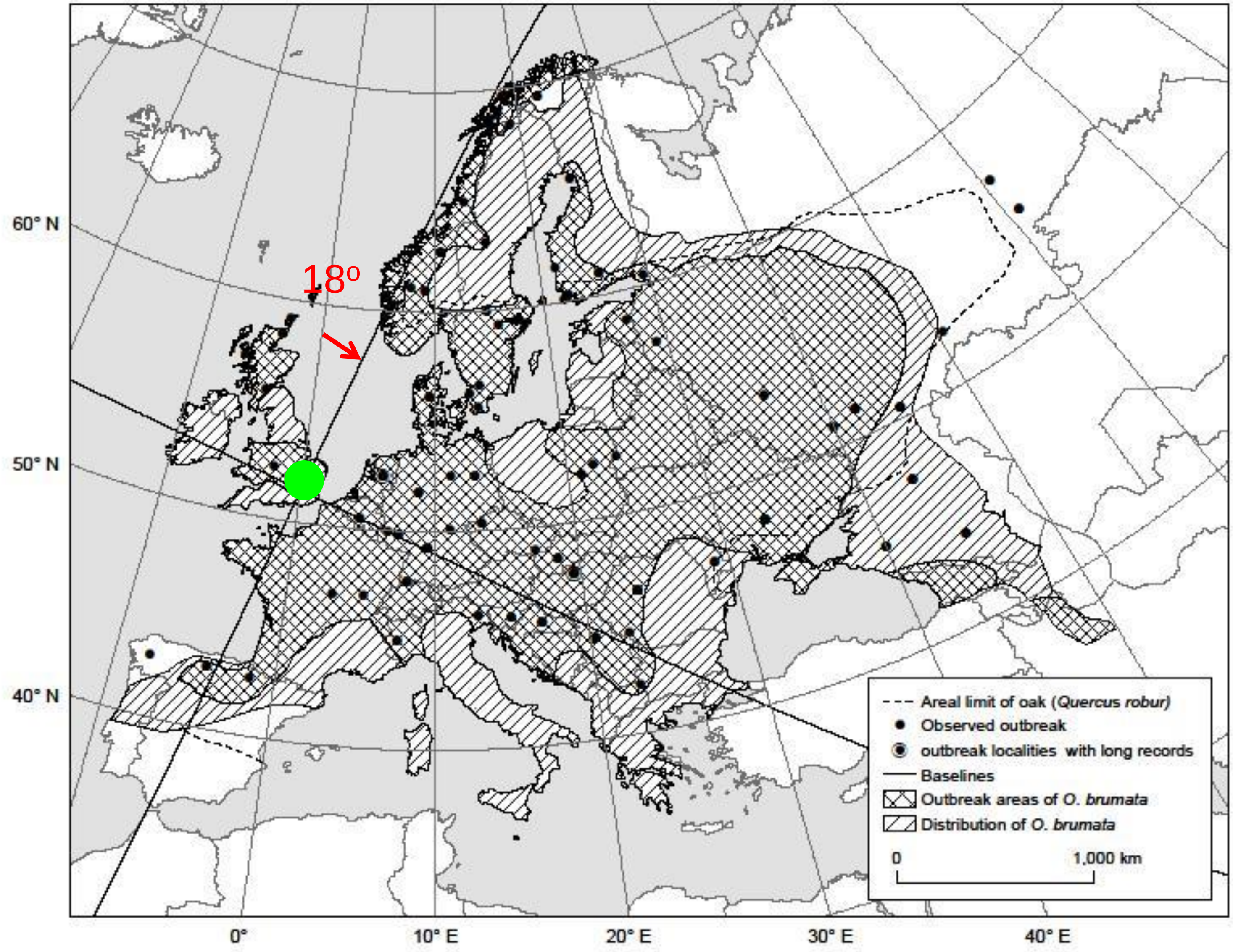


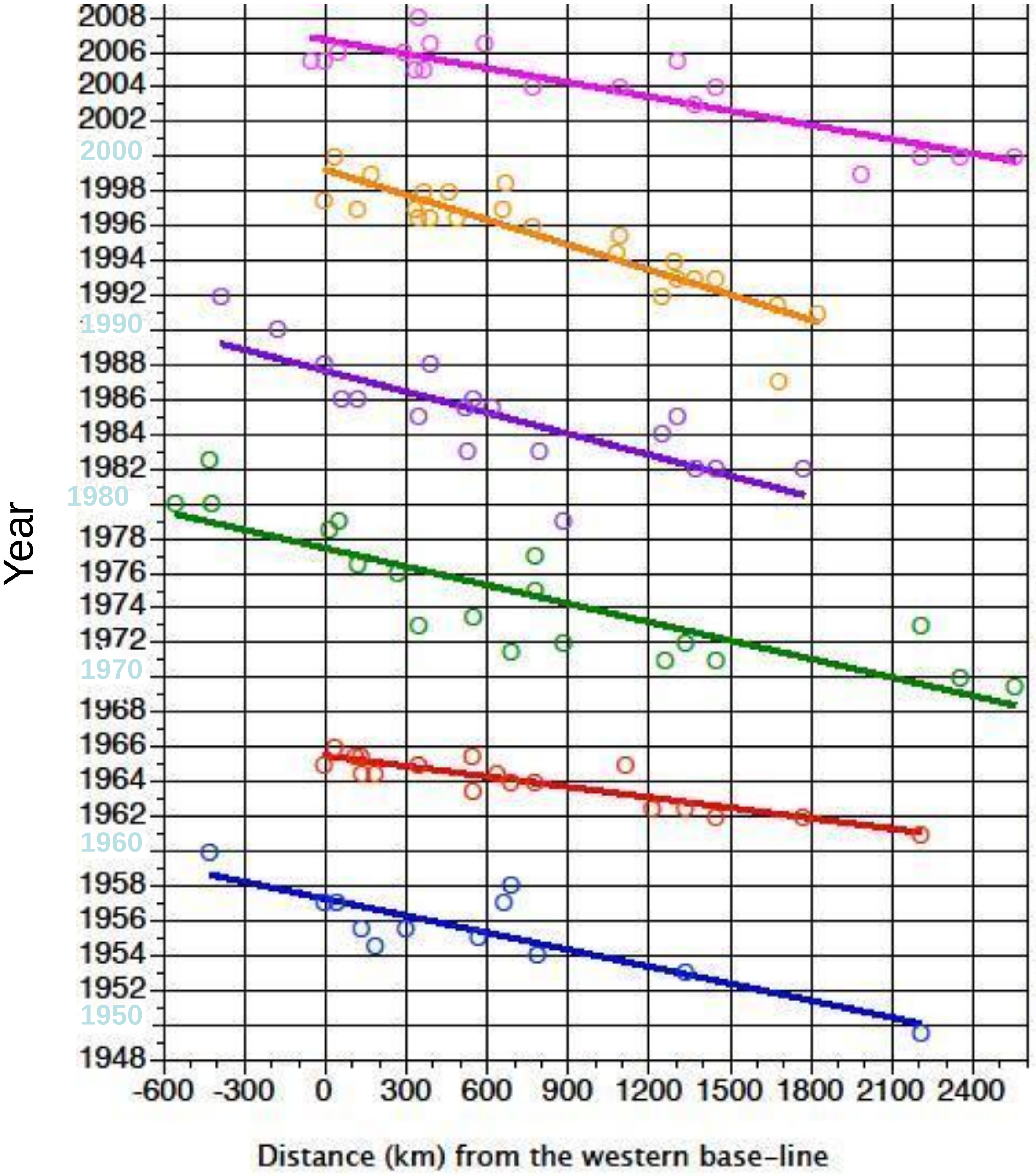
Outbreak range of Operophtera brumata



Methods

- The perpendicular great circles that intersect at Greenwich on the GR80-ellipsoid were rotated 18^o from the true north so the N-S oriented great circle became ~parallel to the Scandes and the North Atlantic coast.


18°
60° N
50° N
40° N
0°
10° E
20° E
30° E
40° E
Areal limit of oak (*Quercus robur*)
Observed outbreak
outbreak localities with long records
Baselines
Outbreak areas of *O. brumata*
Distribution of *O. brumata*
0
1,000 km



2000: $y=-0.002731x+2006.7$; $R^2=0.781$; $p<0.001$

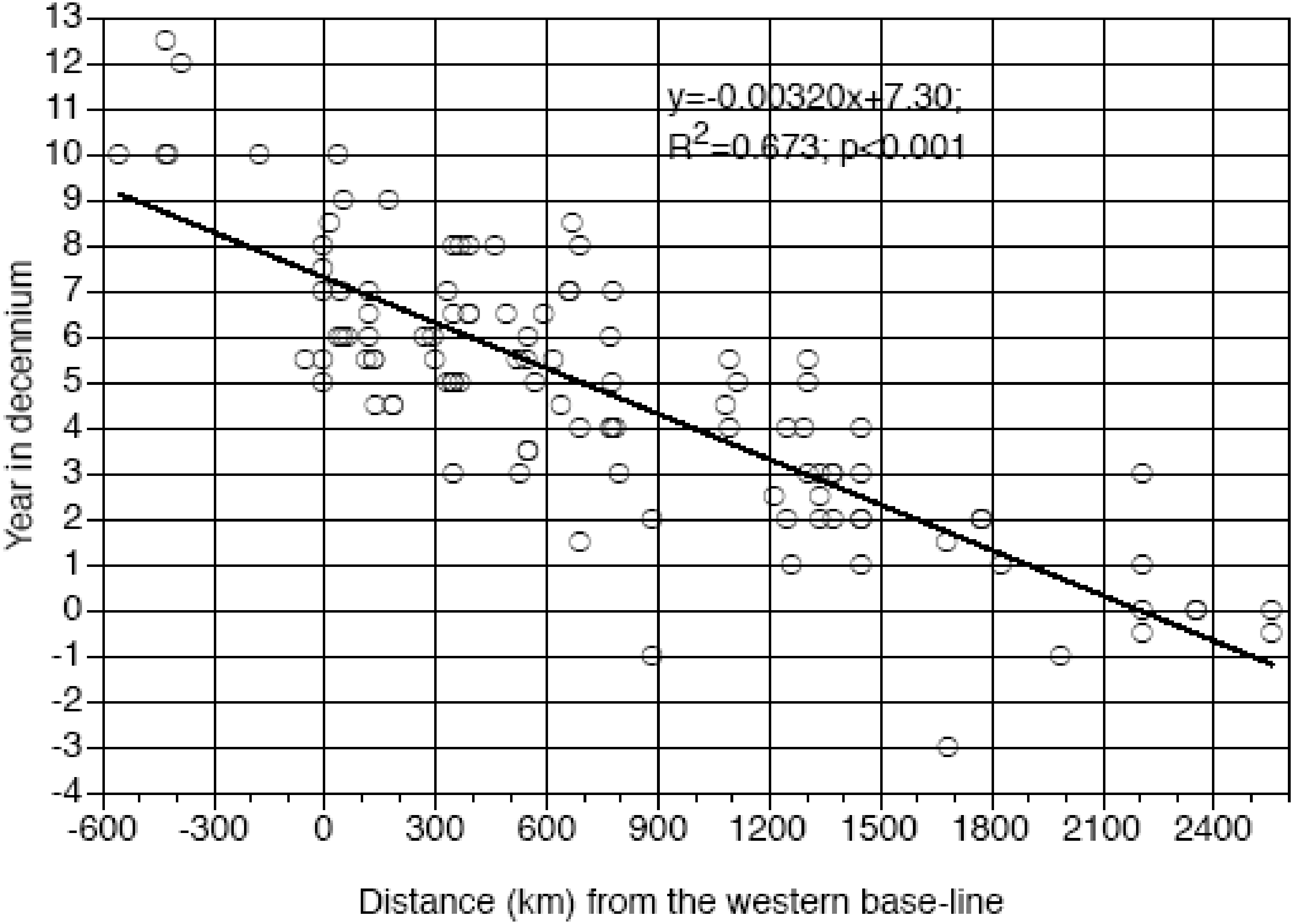
1990: $y=-0.004799x+1999.2$; $R^2=0.803$; $p<0.001$

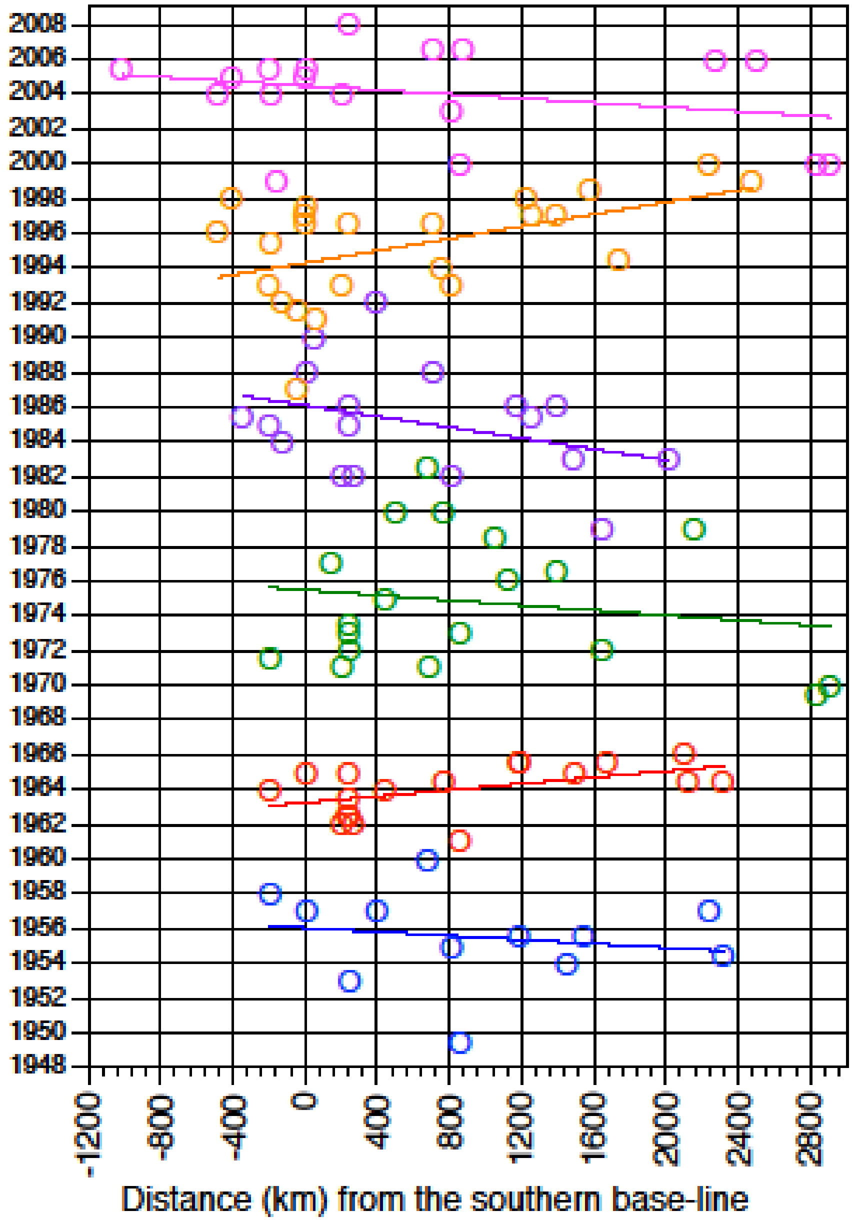
1980: $y=-0.004032x+1987.7$; $R^2=0.612$; $p<0.001$

1970: $y=-0.003540x+1977.4$; $R^2=0.718$; $p<0.001$

1960: $y=-0.002000x+1965.5$; $R^2=0.791$; $p<0.001$

1950: $y=-0.003255x+1957.3$; $R^2=0.716$; $p<0.001$


y=-0.00320x+7.30;
R^2=0.673; p<0.001
Year in decennium
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-600
-300
0
300
600
900
1200
1500
1800
2100
2400
Distance (km) from the western base-line



2000: f(x) = -6.181705E-4*x + 2.004490E+3
R^2 = 7.865144E-2; p=0.26

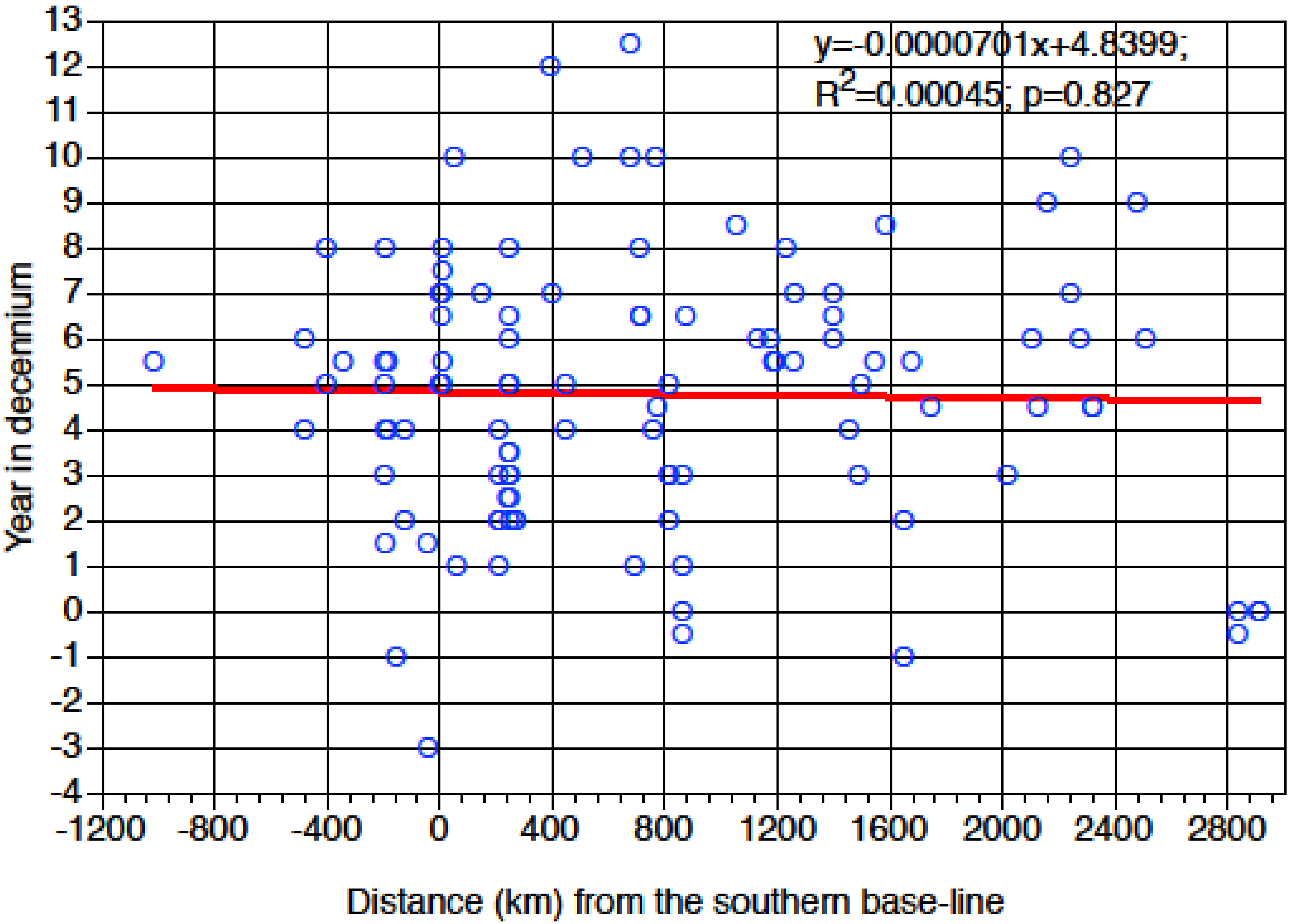
1990: f(x) = 1.741942E-3*x + 1.994298E+3
R^2 = 2.375048E-1; p=0.018

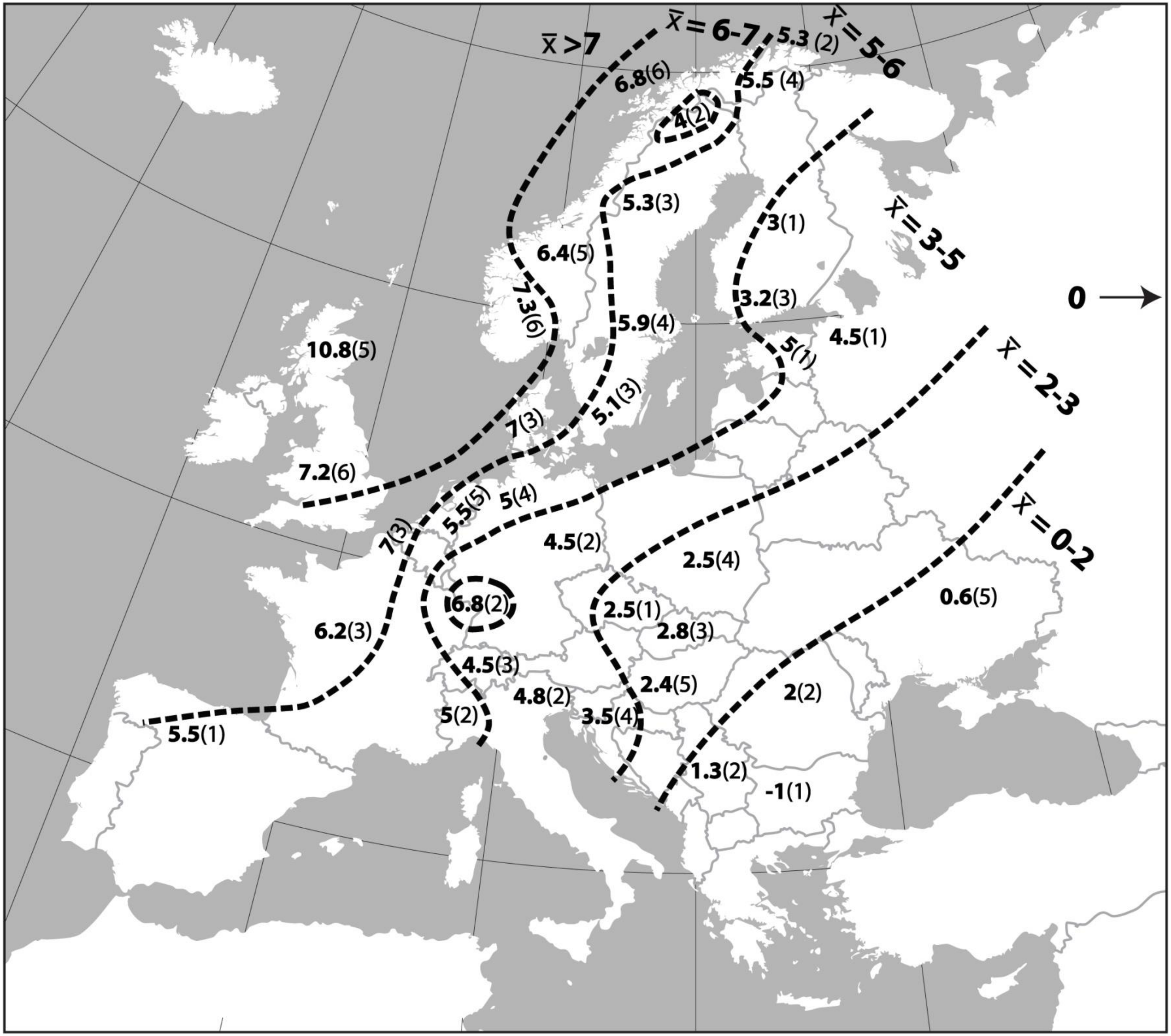
1980: f(x) = -1.568720E-3*x + 1.986094E+3
R^2 = 1.263348E-1; p=0.15

1970: f(x) = -7.250959E-4*x + 1.975476E+3
R^2 = 2.779776E-2; p=0.50

1960: f(x) = 9.034942E-4*x + 1.963251E+3
R^2 = 2.446256E-1; p=0.037

1950: f(x) = -5.722624E-4*x + 1.956052E+3
R^2 = 3.022850E-2; p=0.59


y=-0.0000701x+4.8399;
R2=0.00045; p=0.827
Year in decennium
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-1200
-800
-400
0
400
800
1200
1600
2000
2400
2800
Distance (km) from the southern base-line



$\bar{x} > 7$
$\bar{x} = 6\text{-}7$
$\bar{x} = 5\text{-}6$
5.3 (2)
6.8(6)
5.5 (4)
4(2)
5.3(3)
3(1)
$\bar{x} = 3\text{-}5$
6.4(5)
7.3(6)
3.2(3)
0 →
5.9(4)
4.5(1)
10.8(5)
5(1)
$\bar{x} = 2\text{-}3$
5.1(3)
7(3)
7.2(6)
5.5(5)
5(4)
$\bar{x} = 0\text{-}2$
7(3)
4.5(2)
2.5(4)
6.8(2)
2.5(1)
0.6(5)
6.2(3)
2.8(3)
4.5(3)
2.4(5)
2(2)
4.8(2)
5(2)
3.5(4)
5.5(1)
1.3(2)
-1(1)

Why lagged synchrony and waves?

Reaction-diffusion models:

- **trophic interactions** - Dispersal prey or natural enemies or plant-herbivore interactions.
- Boundaries with hostile environment:

  a) Eastern climatic boundary

  b) Eastern limit of regular oak distribution

Population growth model

applicable with long data sets

$R = \ln (N_t / N_{t-1})$

where N_t =

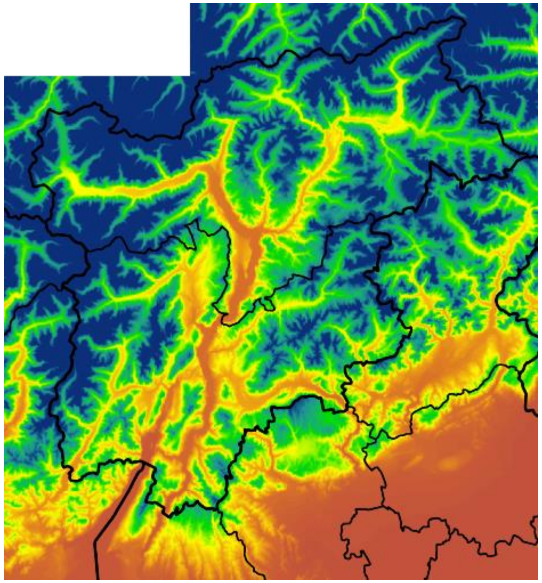
- Number of individuals per unit area in year t
- Number of infested trees per unit area in year t
- attacked area of year t
- ….

Long-term survey of *Thaumetopoea pityocampa* population dynamics in the Italian Alps

Objectives

Identify endogenous and exogenous factors driving the population dynamics in Trentino Alto Adige, a mountain area where the pest is present since many years.

1. Assemble survey data
2. Apply a population model
3. Test climatic factors



Orange to green: 90 to 1450 m of altitude

Materials and methods

Two time-series of attacked area surveys: twenty years in Trentino (from 1990 to 2009) and thirty-seven in Alto Adige (from 1975 to 2011).

Altitude span: 91 – 1450 m

Host species: Pinus sylvestris and Pinus nigra

Host area: 20,740 ha (Trentino), 24,864 (Alto Adige)

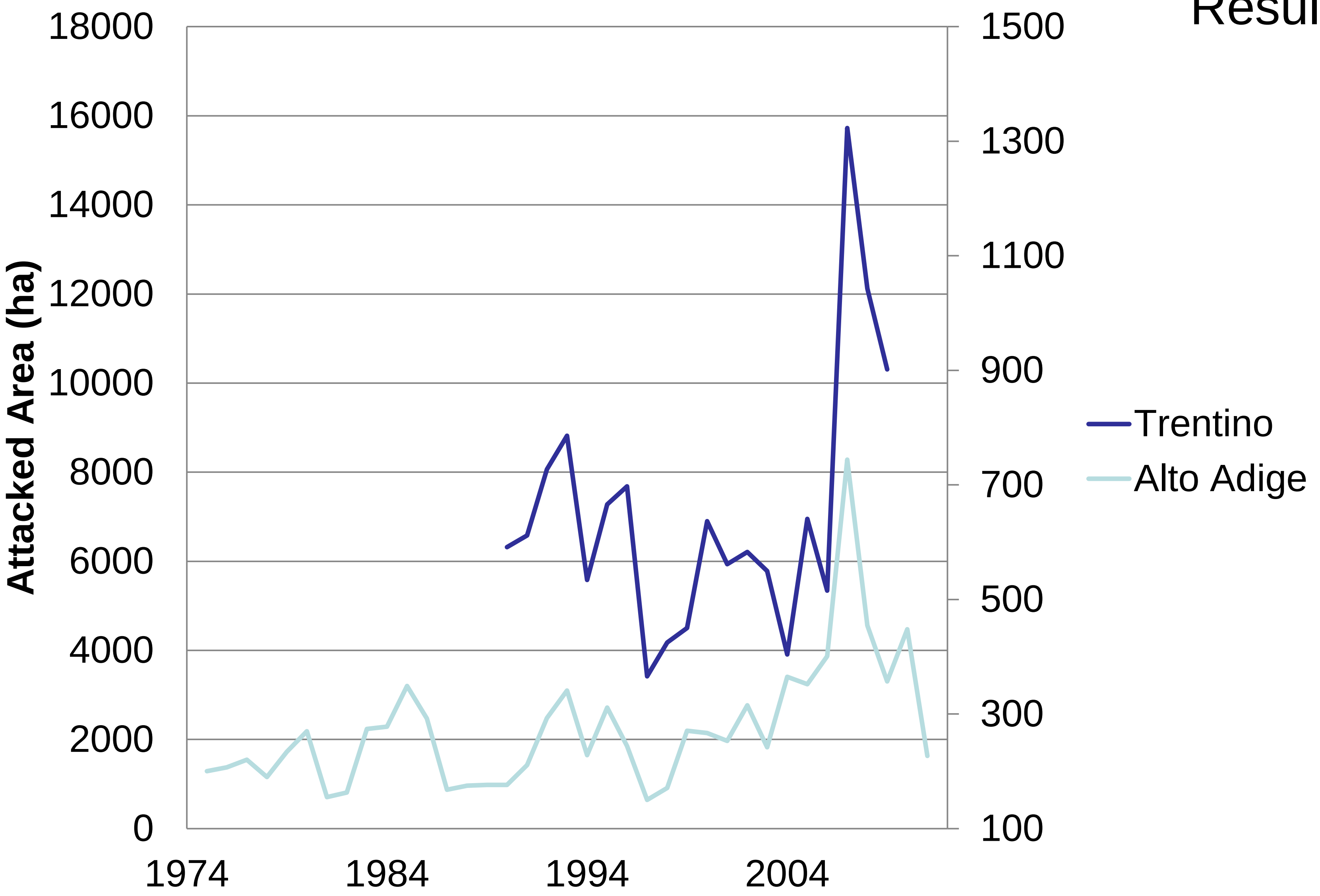
Climate: T-Winter min t-1, T-Summer, R-Spring, R-Autumn

Model
Population growth rate as per capita rate of increase
$R = \ln (N_t/N_{t-1})$ (where N_t= attacked area of year t)

$R = f(N_{t-1,} N_{t-2,} \dots) + \varepsilon$ with ε representing sampling error plus exogenous (i.e. density independent) effects

N_{t-1} → host plant related factors (shortage, quality, competition)
N_{t-2} → natural enemies related factors (higher delay)

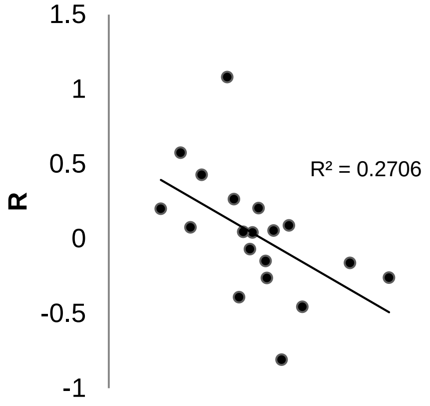
Results 1

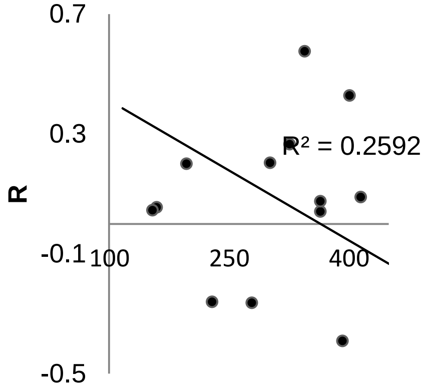


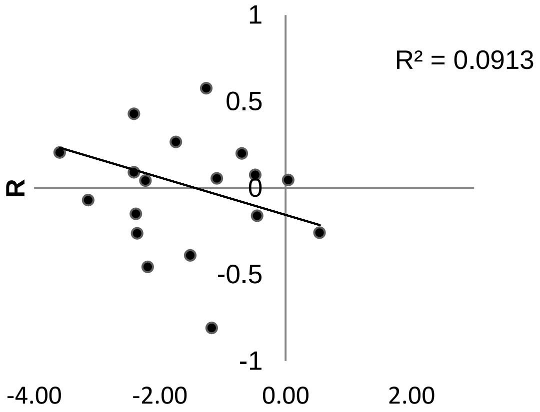
Population fluctuations in Trentino and in Alto Adige (vertical scale on the left is referred to Trentino attacked area, on the right to Alto Adige, in hectares).

Trentino BEST MODEL : 51% of variance explained

Factors	%
Density N t-1	27
Autumnal Rainfall	26
Min Winter Temperature t-1	9

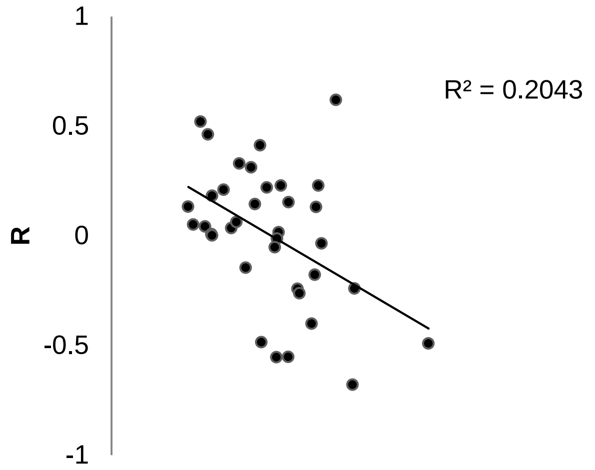


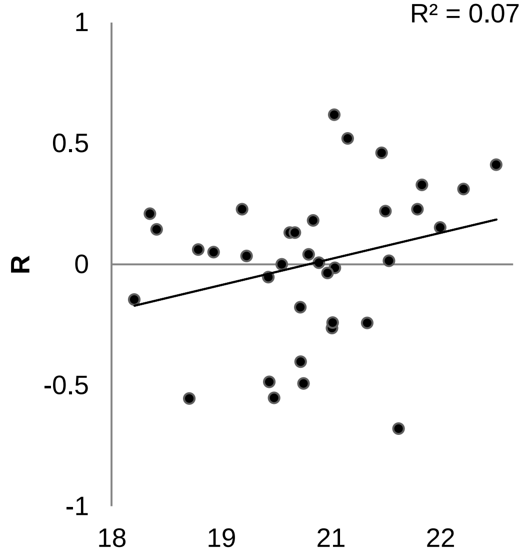




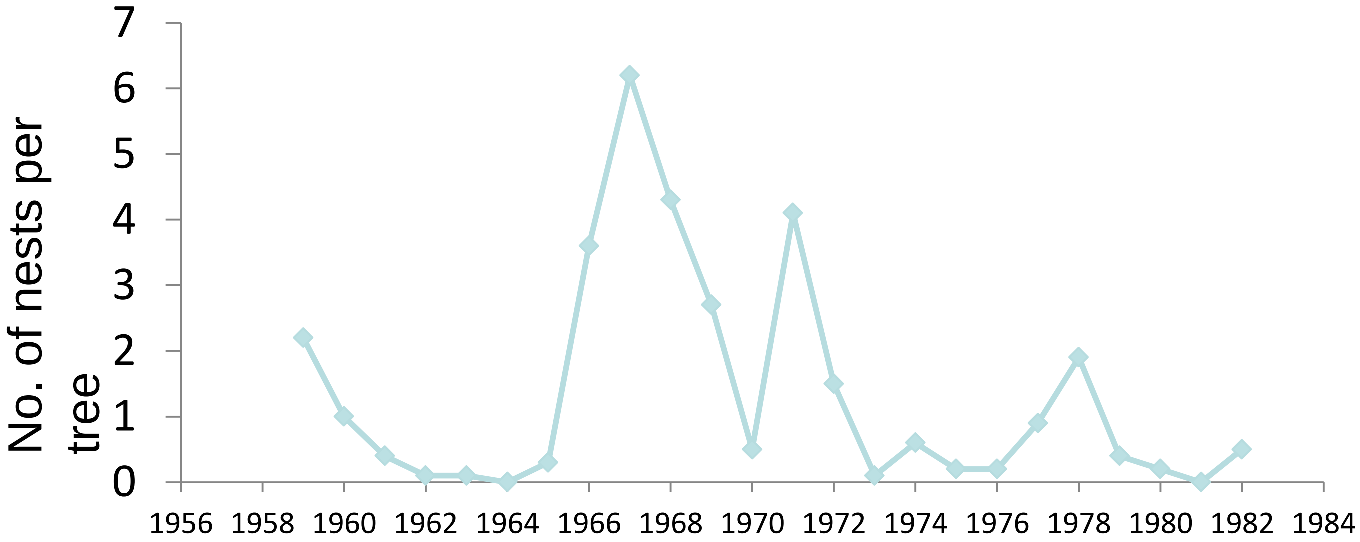
Alto Adige BEST MODEL : 27% of variance explained

Factors	%
Density N t-1	20
Summer Temperature	7





Comparison with other historical series: Mont Ventoux 1959-1982 (Geri 1983)



Availability of other historical series?
Standardization of the data needed.

Preliminary conclusions

- Consistency of the pattern between Trentino and Alto Adige
- Density in the previous year as main driving factor of the population dynamics → emphasis on the regulation by the host plant (food quantity and quality)
- Delayed density-dependence by natural enemies not significant in the area
- Climatic factors important at local scale