

Continental molluscs facing environmental changes



Palaeobiodiversity and distribution of Quaternary European continental snails in response to climatic cyclicality

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A Modern vegetation

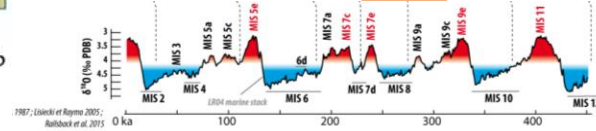
Ice	Boreal forest	Mediterranean scrub
Tundra and mountain	Deciduous and conifer forest	Prairie-steppe



B Glacial vegetation

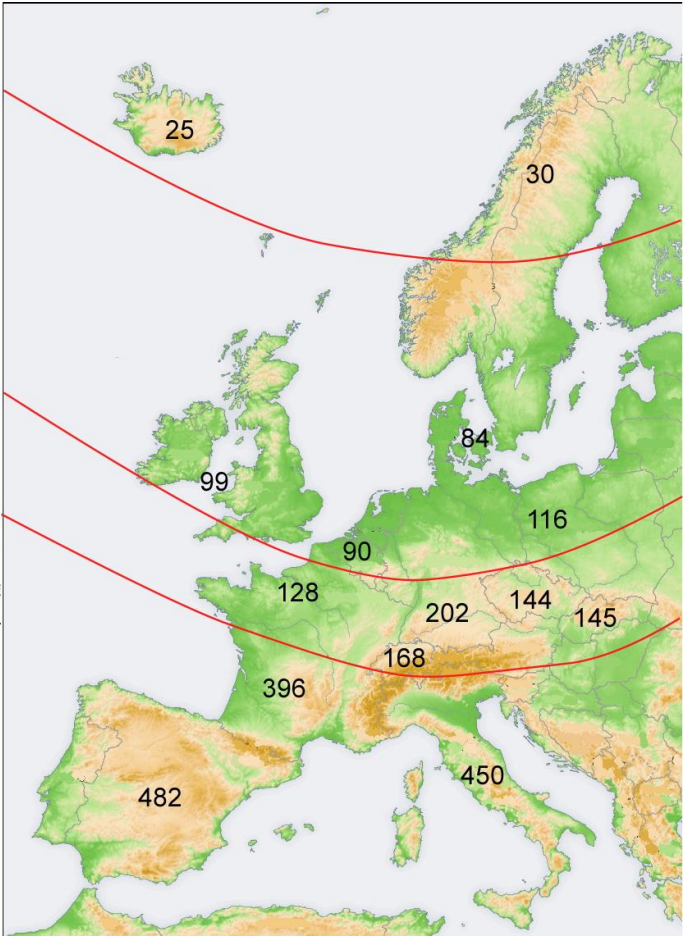
Since Middle Pleistocene
Climatic cycles = 100kyr

Interglacial: 20/30 kyr



Glacial: 70/80 kyr

Diversity
Distribution



European land snails (non slugs): number of species

Contribution of malacofaunas to Quaternary studies

Palaeoenvironment reconstruction

Biostratigraphy/Biogeography

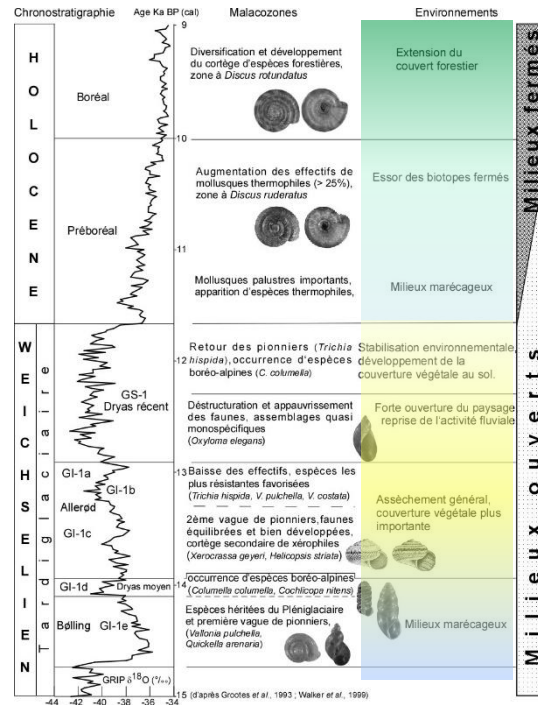
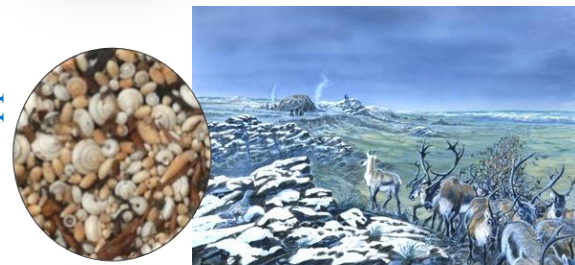
Landscape, climate

Chronology

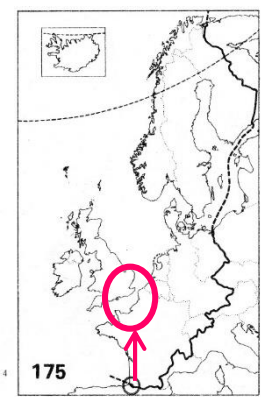
Interglacial Forest



Glacial Steppe



MIS11

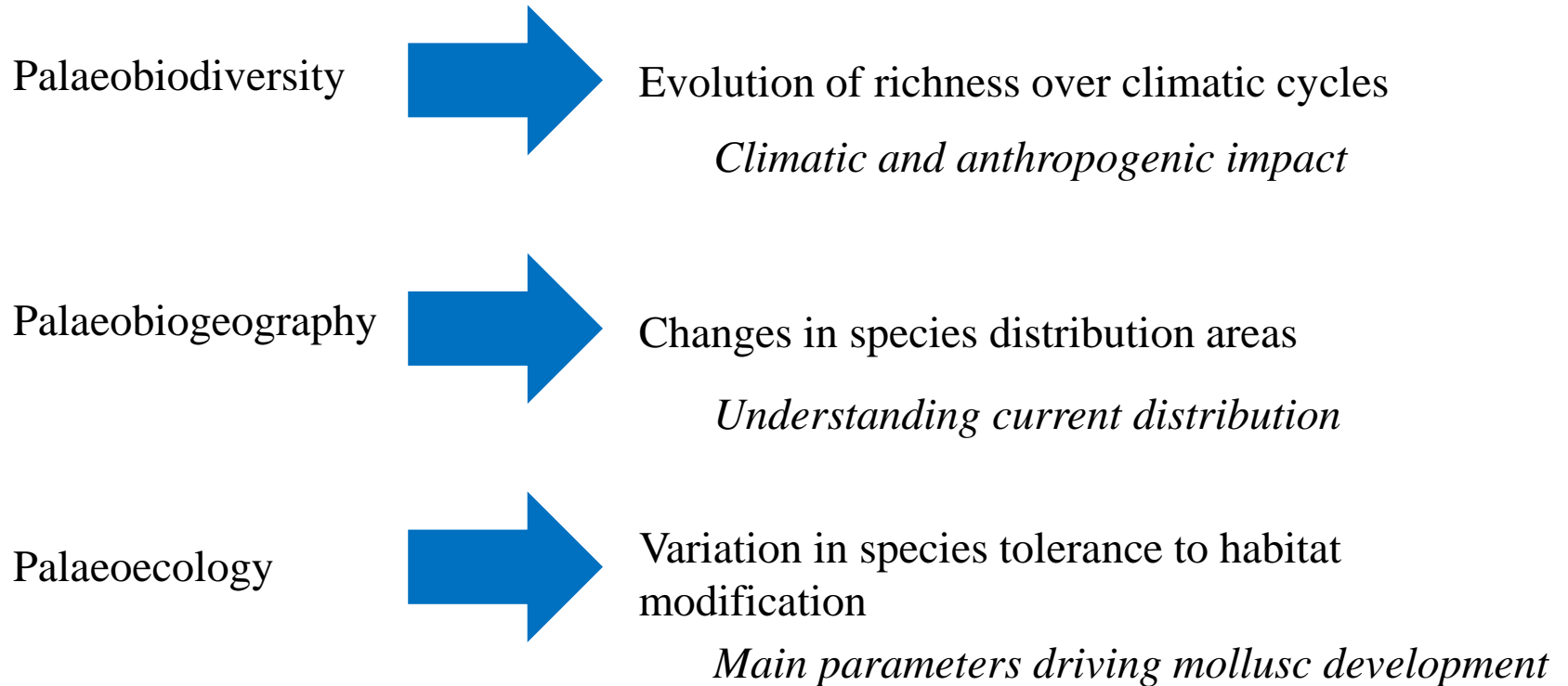


175

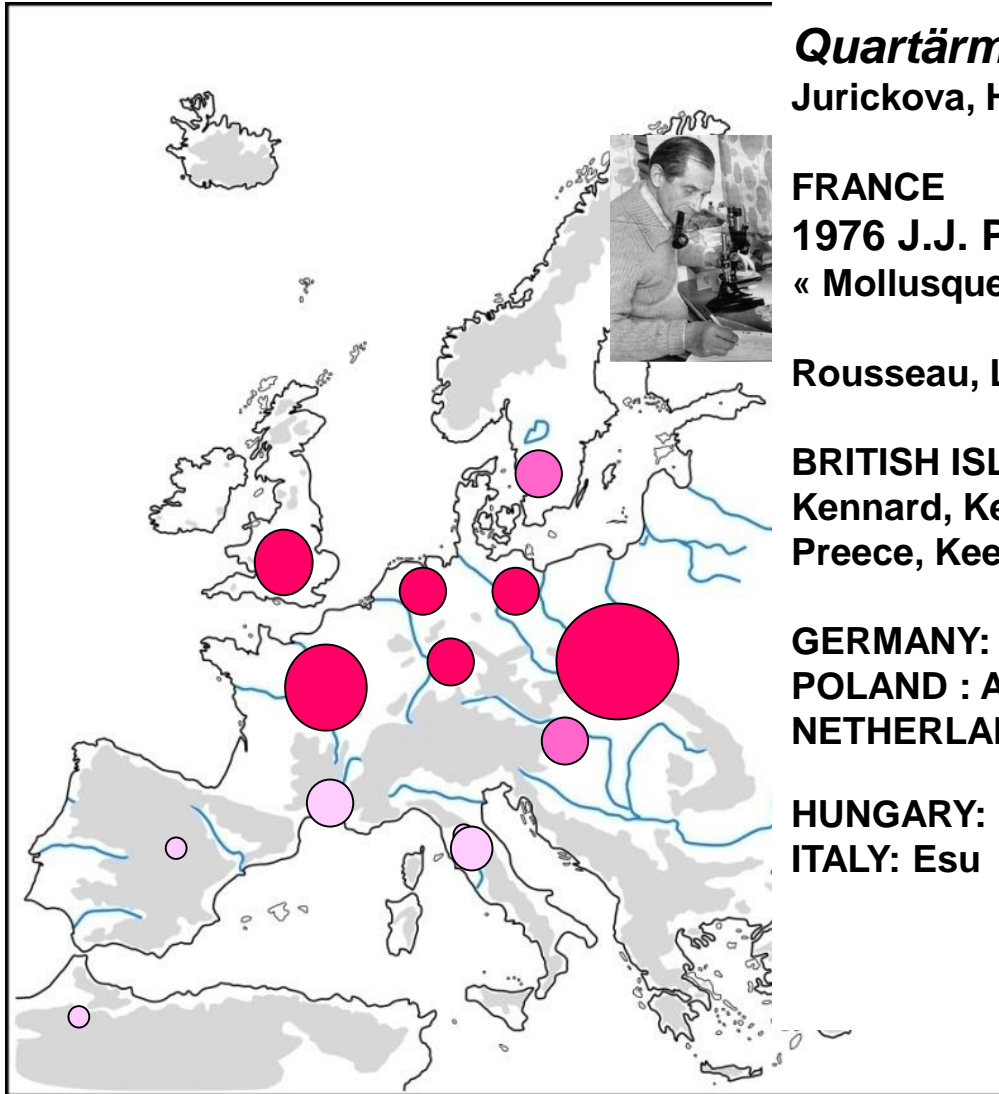
Milieux fermés / Milieux ouverts

15 (d'après Grootes et al., 1993; Walker et al., 1999)

Contribution of Quaternary molluscan studies to malacology



Quaternary malacology in Europe: history of research



CZECH REPUBLIC & SLOVAQUIA:

Vojen LOZEK 1964



Quartärmollusken der Tschechoslowakei
Jurickova, Horsak...

FRANCE

1976 J.J. Puisségur

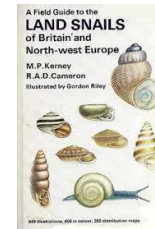
« Mollusques continentaux quaternaires de Bourgogne »

Rousseau, Limondin-Lozouet, Moine, Granai....

BRITISH ISLES

Kennard, Kerney, Evans, 1970

Preece, Keen, 1980



GERMANY: Mania, Münzig.....

POLAND : Alexandrowicz, Szymanek...

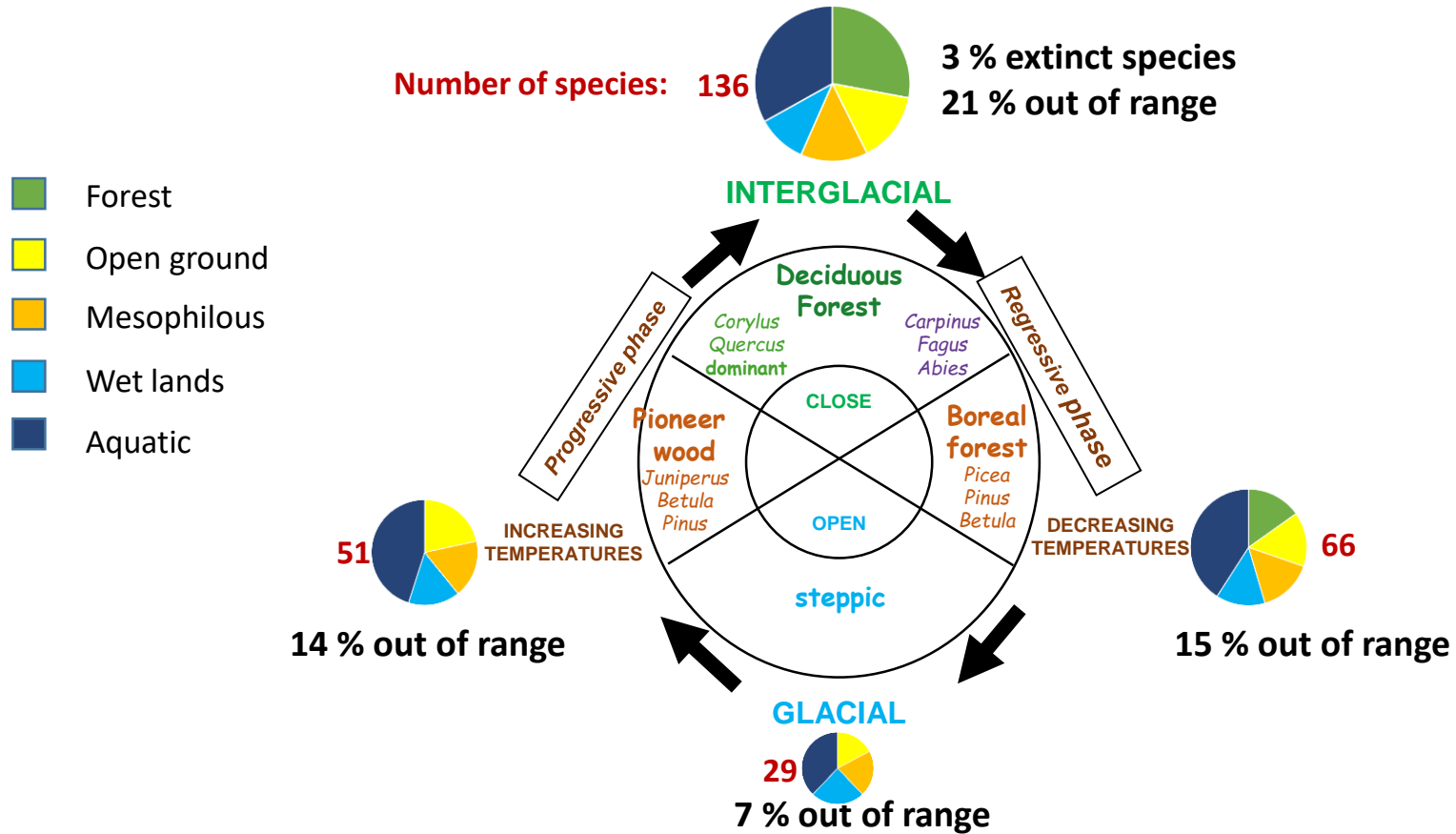
NETHERLANDS: Meijer

HUNGARY: Krolopp, Sumegi...

ITALY: Esu

Mid latitudes studied since the 60's
Southern Europe: still a lot to do

Temperate Europe: species diversity within a climatic cycle vs vegetation development



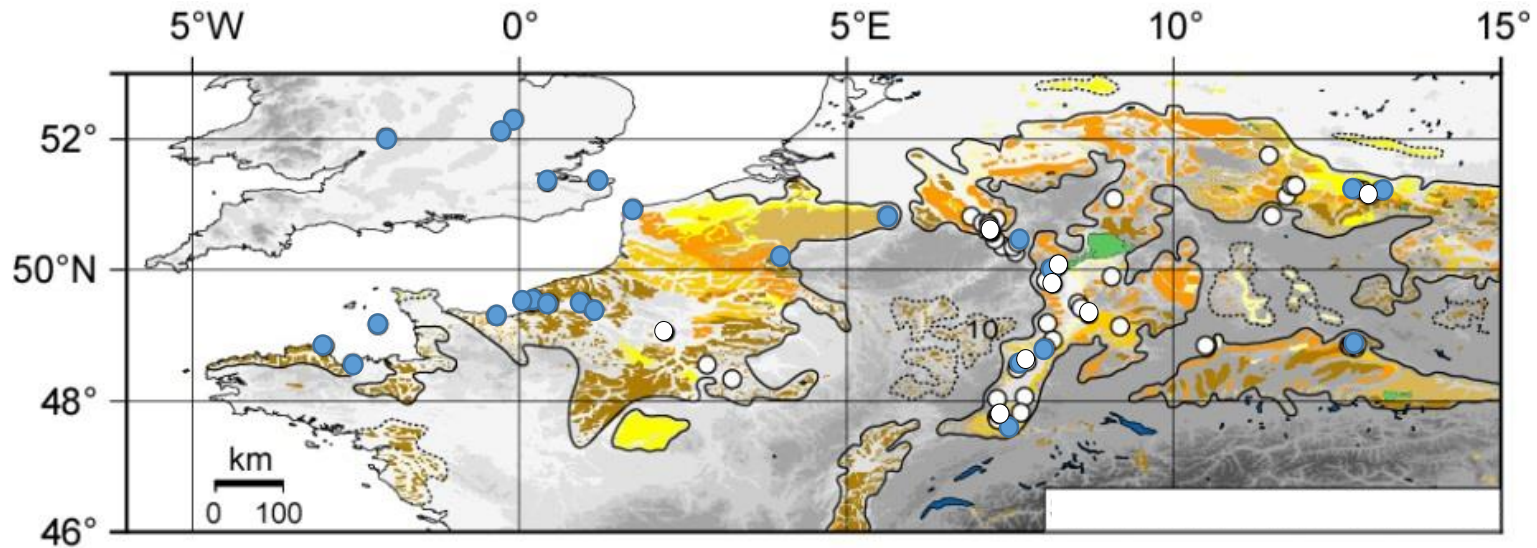
Who moves and when ?

Example of the Somme valley: 1 Myr, 34 sites, 300 samples

Glacial land snails faunas

Loess deposits, low diversity (5 to 20 sp/site), open environments

Weichselian Upper Pleniglacial : East/West diversity gradient



West: 5 species

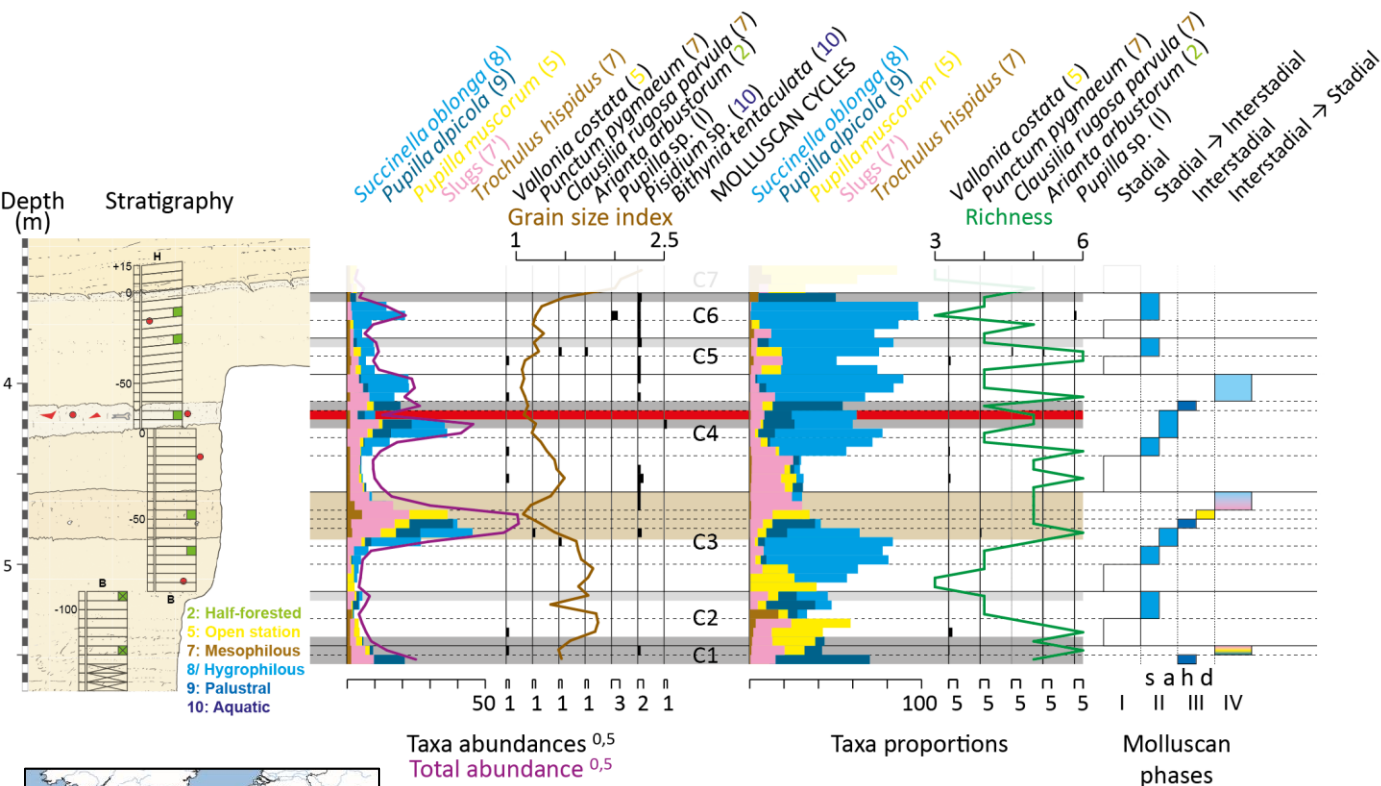
- *Columella columella*, *Pupilla muscorum*, *Succinea oblonga*, *Trichia hispida*, slugs

- Aegopinella nitens*, *Abida secale*, *Arianta arbustorum*, *Bradybaena fruticum*, *Carychium minimum*, *Candidula unifasciata*, *Chondrula tridens*, *Clausilia dubia*, *Clausilia parvula*, *Cochlicopa lubrica*, *Columella columella*, *Columella edentula*, *Discus rotundatus*, *Eucoberesia diaphana*, *Euconulus fulvus*, *Helicopsis striata*, *Jaminia quadridens*, *Neostyriaca corynodes*, *Nesovitrea hammonis*, *Orcula dolium*, *Oxyloma elegans*, *Punctum pygmaeum*, *Pupilla alpicola*, *Pupilla loessica*, *Pupilla muscorum*, *Pupilla sterri*, *Pupilla triplicata*, slugs, *Succinea oblonga*, *Trichia hispida*, *Trichia sericea*, *Trichia striolata*, *Vallonia costata*, *Vallonia pulchella*, *Vallonia tenuilabris*, *Vertigo genesii*, *Vertigo parcedentata*, *Vertigo pygmaea*, *Vitrea crystallina*

East: 39 species



Glacial land snails faunas: Interstadial cyclicality during Upper Weichselian (30-26 kyr)



Moine et al. (JQS, 2021)



P. muscorum/Slugs

decline of palustral+slugs
= temperature high, drier
interstadial optimum

media.nationalgeographic.org



P. alpicola

Palustral taxa, max total abundance
= max temperature interstadial optimum

icestories.exploratorium.edu



T. hispidus/*C. parvula*

Increase hygrophilous+taxa Rhine valley
= milder, more humid, vegetation diversified
transition stadial/interstadial

ad.wikimedia.org



P. muscorum/*S. oblonga*

Open land+hygrophilous
= poor vegetation+cold stadial

aquaportail.com
and www.aquaportail.com

Glacial land snails faunas

Important impoverishment in diversity

There is an evolutionary dynamic of malacofauna in response to climatic cyclicity over large geographical areas

No specific assemblages are linked to particular glacial periods

During interstadial periods, malacofauna show repeated dynamics in the order of arrival and development of species

High resolution sampling is essential to perceive these variations

Lateglacial land snails faunas

The process of recolonization

The Late-Glacial/Holocene transition in North-West Europe

Fluvial deposits

Increasing diversity: 12/20 species

Abundance follows temperature curve

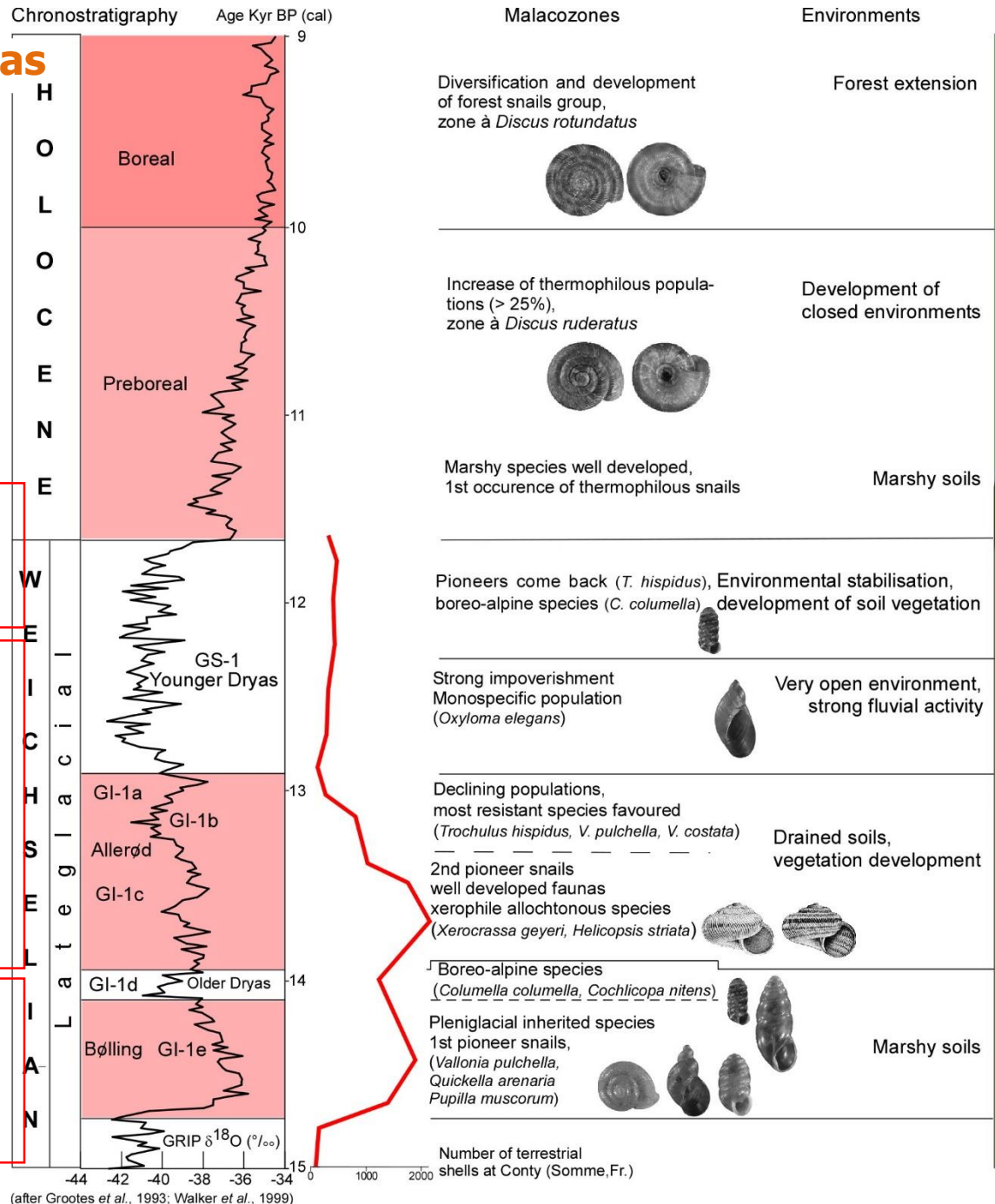
Each climatic episode = singular malacological signature

Boreo-alpine species, during stadials

Pioneer species, tolerant to open habitats
(*Q. arenaria*, *C. nitens*, *V. genesii*, *C. columella*, *H. striata*, *T. geyeri*)

P. muscorum in earliest wet habitats

Strict thermophilous species occur only at the edge of the Holocene



(after Grootes et al., 1993; Walker et al., 1999)

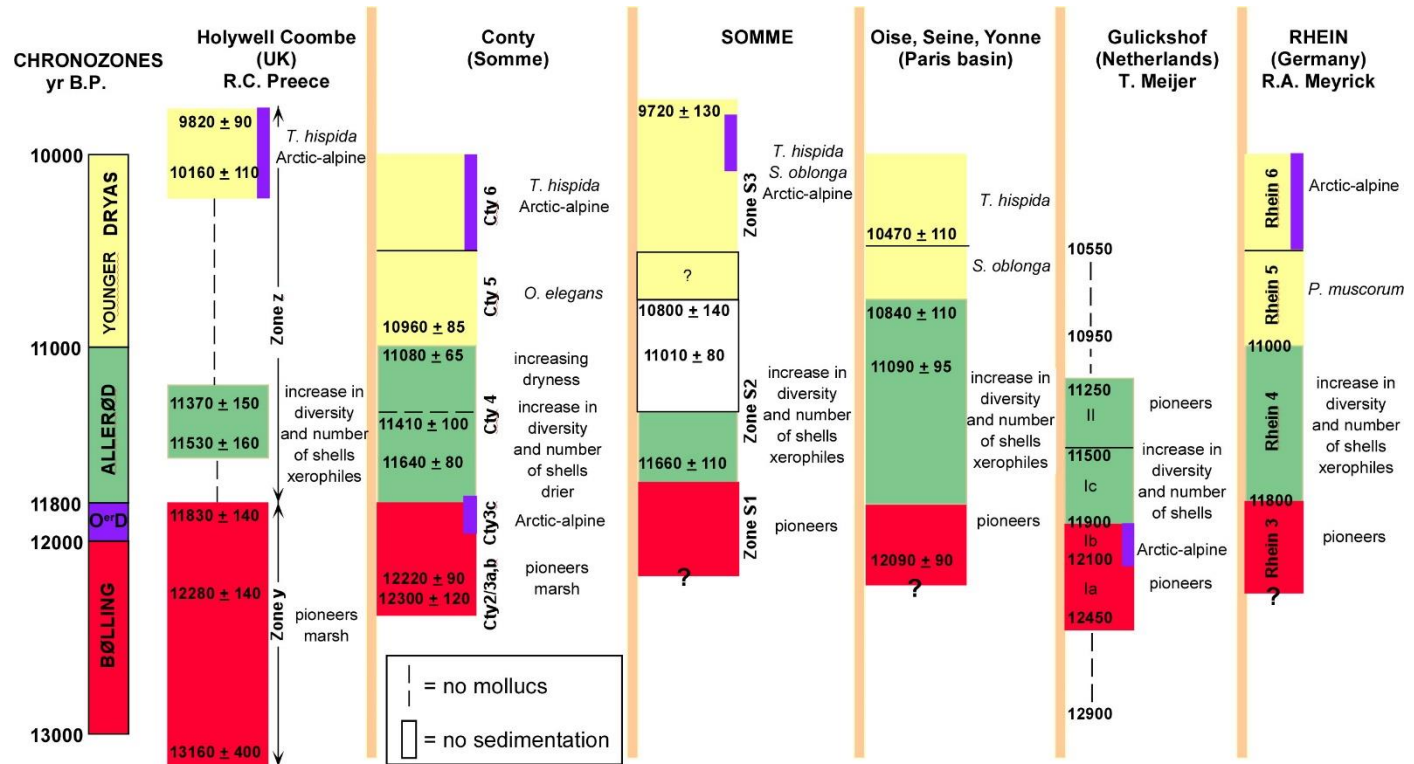
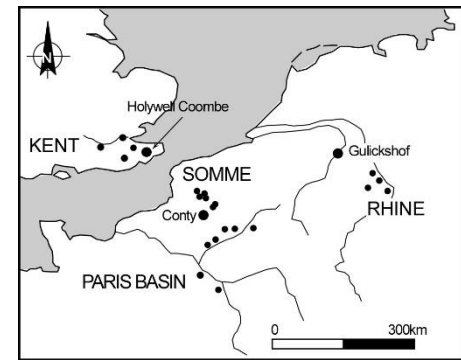
Lateglacial land snails faunas

The process of recolonization

Regional differences in diagnostic species

BUT

Similar and synchronous dynamic of malacofauna in response to climatic variability over large geographical area



NORTH-WEST EUROPE : LATEGLACIAL MALACOLOGICAL BIOZONES

Lateglacial land snails faunas

The process of recolonization

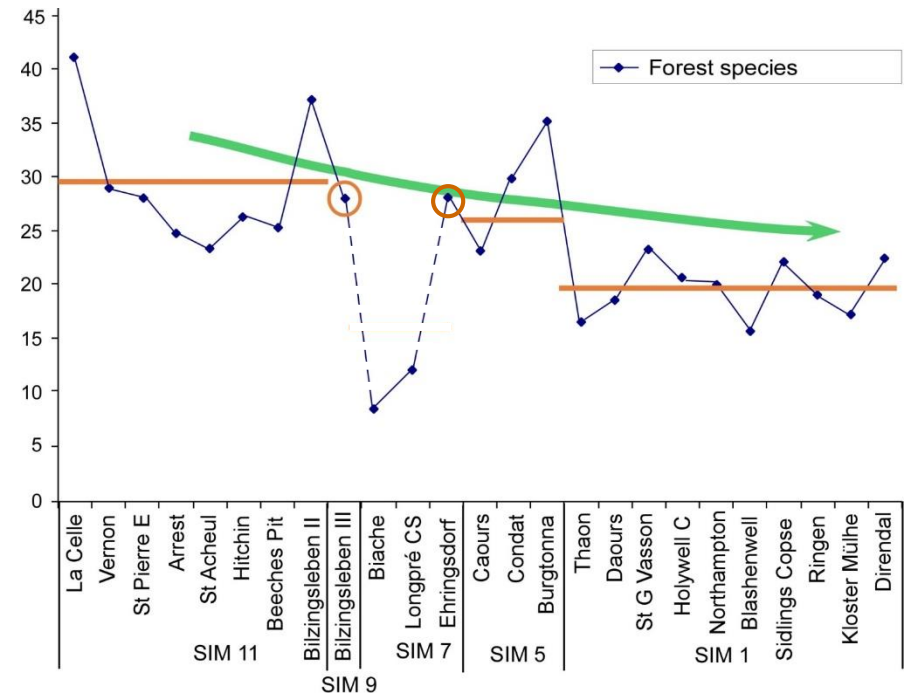
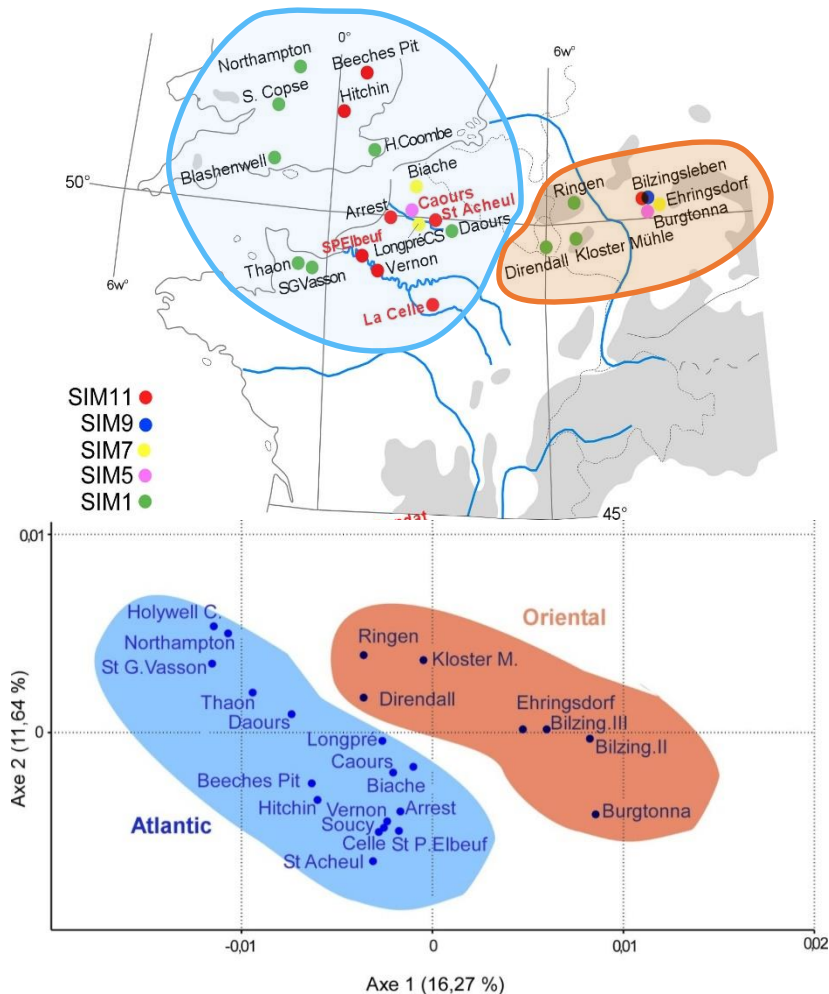
Temperature is an important driver of diversity and abundance of malacofaunas

Arrival of species is strongly dependent on distance from refugial areas

Some species may have an opportunistic behavior

Lateglacial malacological succession provide a good biostratigraphical reference

Interglacial tufas with malacofaunas in North West Europe



Forest species = key factor to identify itgl optima, decreasing tendency

When compared at the scale of NW Europe itgl tufa malacofaunas appear divided into two groups according to specific composition

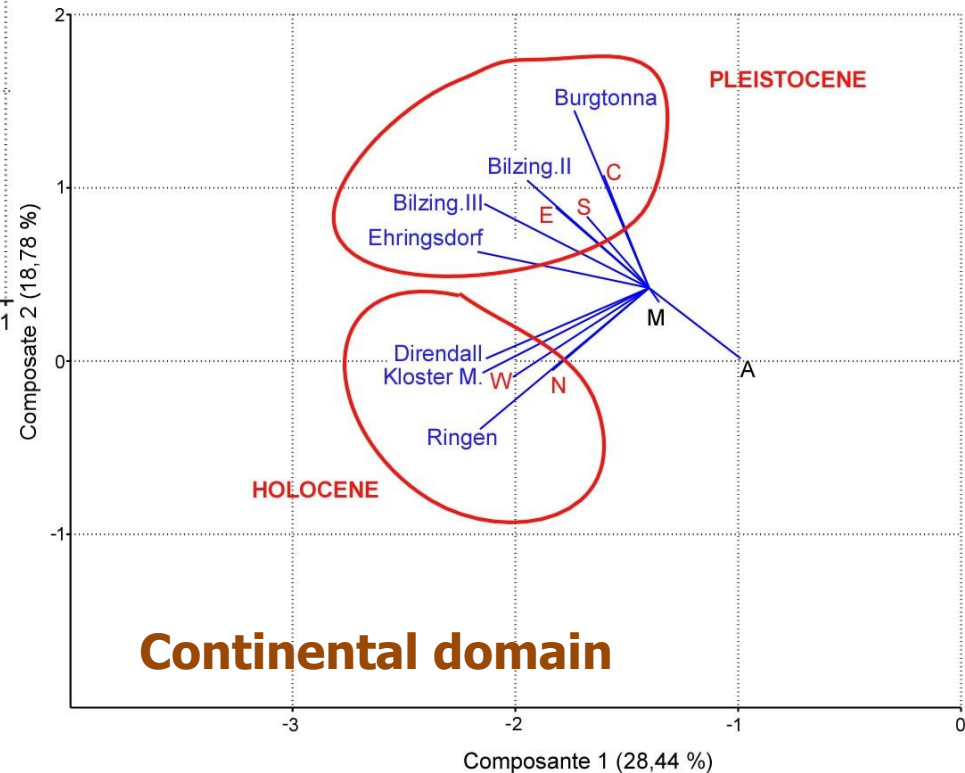
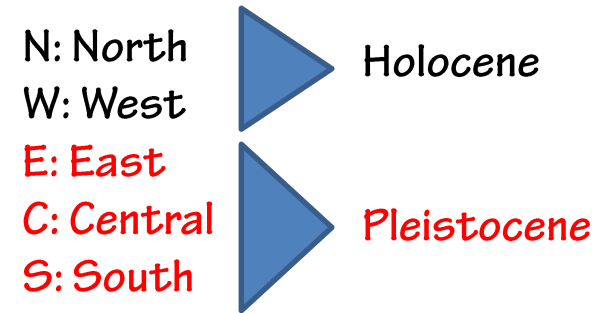
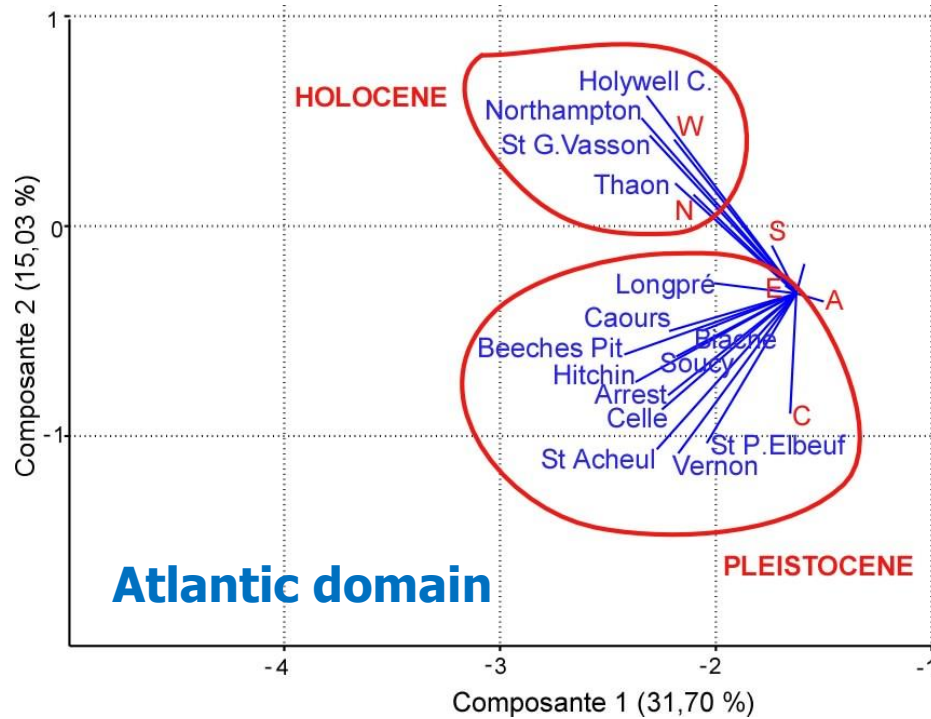
Multivariate 1 : geography

Which are the missing species ?

Pleistocene and Holocene malacological assemblages versus modern geographical range of forest species

Further analyses of composition of malacofaunas taking into account geographical range of species give the same result for both biogeographical domains

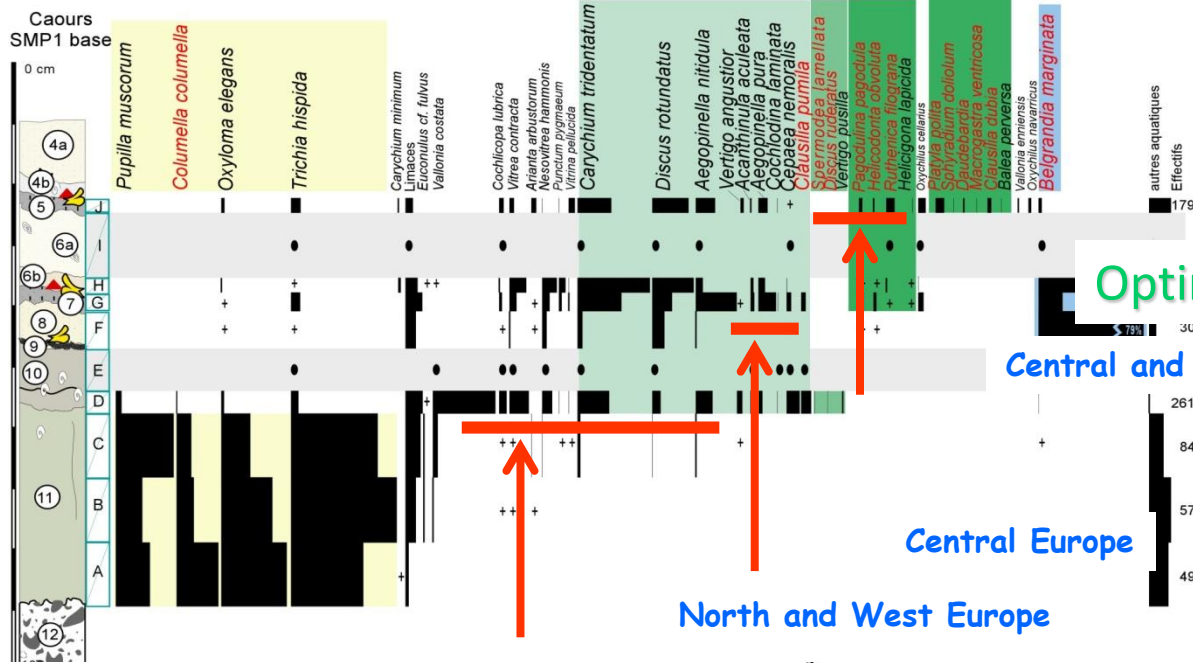
Multivariate 2 : time and range



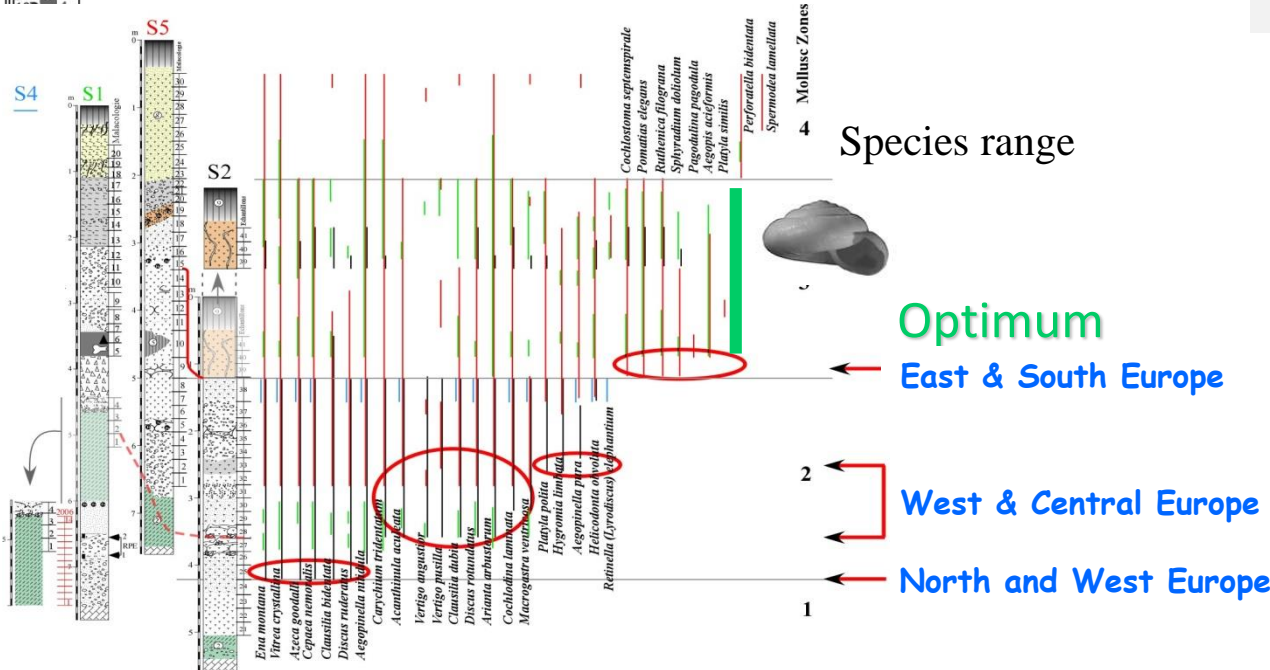
Why is there a loss of species during the Holocene?

Pleistocene interglacials: succession of forest malacological assemblages

MIS 5



MIS 11



Optimum

Central and South Europe

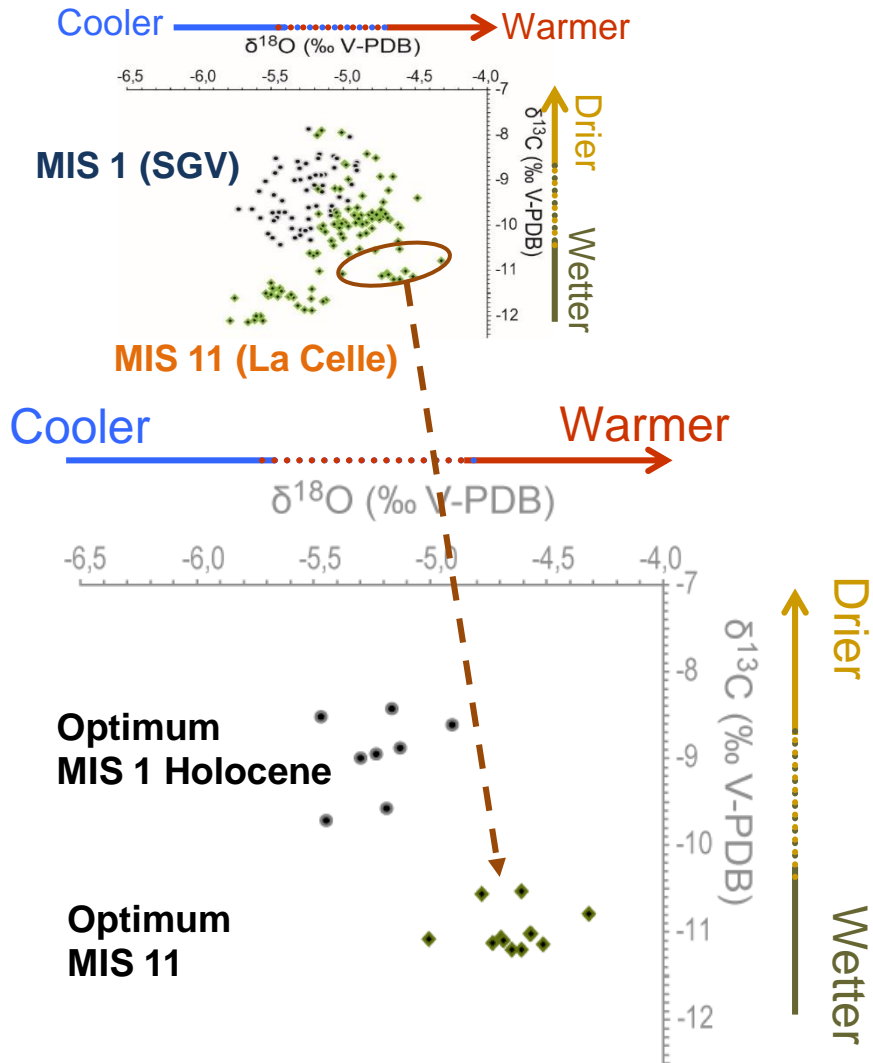
Central Europe

North and West Europe

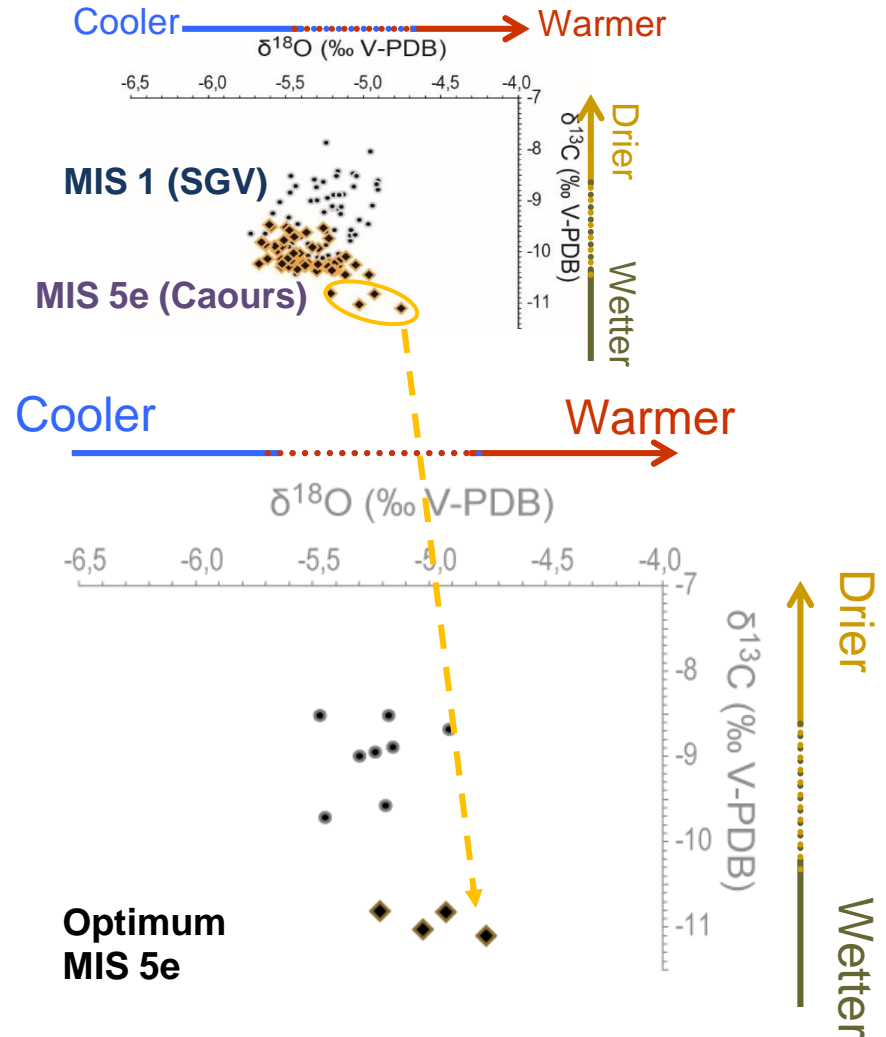
Mollusc migration ends at optima

Geochemical data on tufa deposits = evolution of climatic parameters

Holocene vs MIS 11

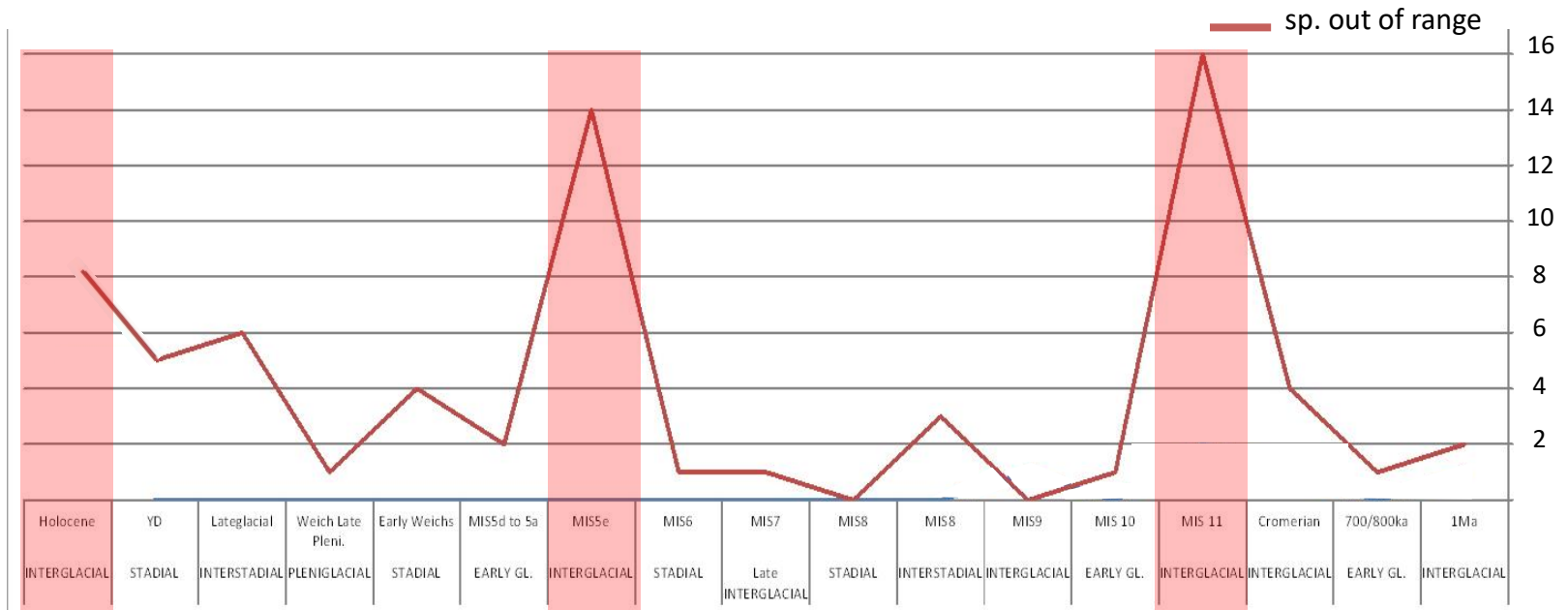


Holocene vs MIS 5e



The Holocene climatic optimum is significantly less humid than those of Pleistocene interglacials

Species out of range Interglacial malacological signatures



Species out of range are present during all climatic phases

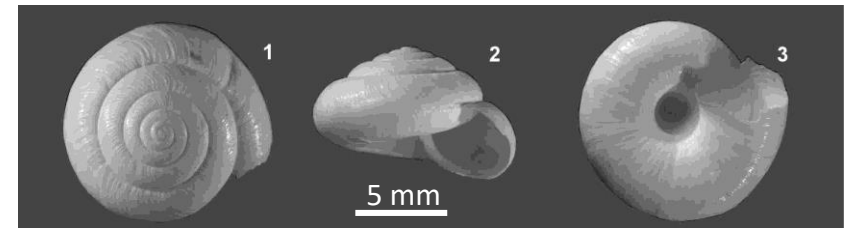
Higher numbers of species out of range occur during Interglacials

Example of the Somme valley: 1 Myr, 34 sites, 300 samples

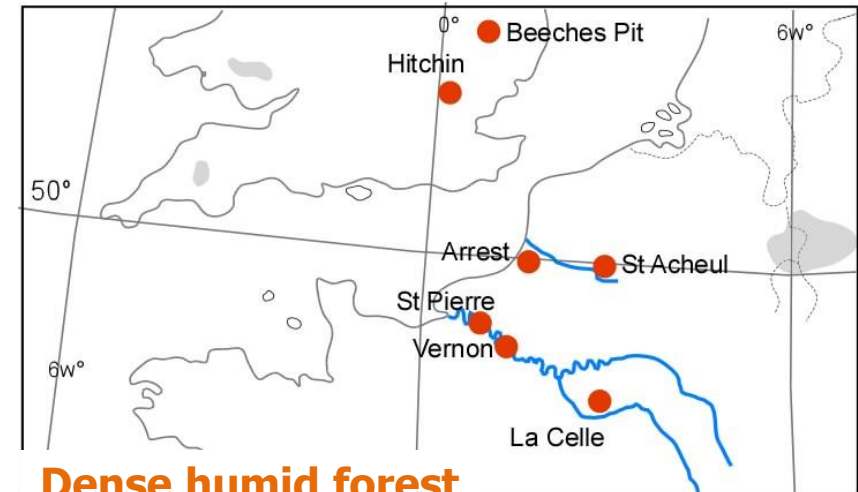
The MIS 11 (400 kyr) *Lyrodiscus* fauna

biostratigraphic key for MIS 11 sites of NW Europe

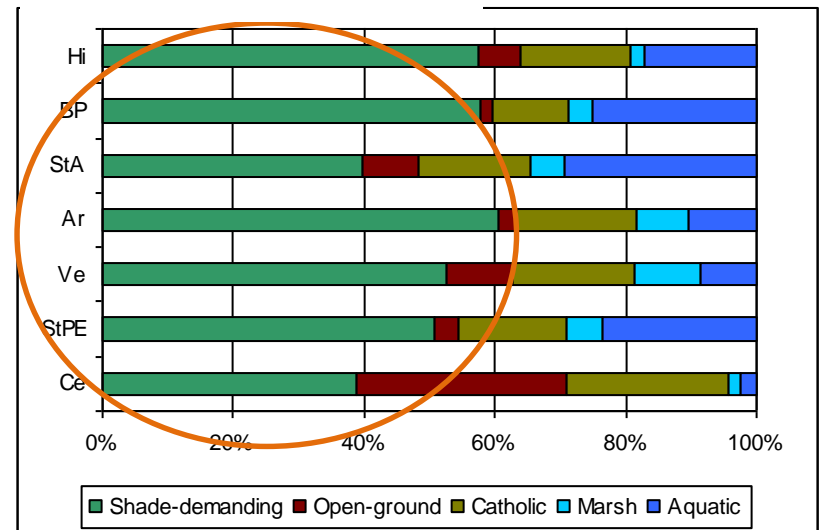
	StPE	Ve	Ce	Ar	StA	BP	Hi
Espèces allochtones							
<i>Platyla polita</i>	x	x	x		x	x	x
<i>Platyla similis</i>	x	x	x			x	x
<i>Ena montana</i>	x	x	x	x	x	x	x
<i>Leiostyla anglica</i>		x				x	x
<i>Discus ruderatus</i>		x	x	x		x	x
<i>Macrogastra ventricosa</i>	x	x	x	x	x		x
<i>Macrogastra plicatula</i>	x						
<i>Laciniaria biplicata</i>	x	x					
<i>Ruthenica filigrana</i>		x	x		x	x	x
<i>Laminifera pauli</i>	x		x			x	x
<i>Clausilia pumila</i>					x	x	x
<i>Clausilia dubia</i>			x	x	x		
<i>Cochlodina orthostoma</i>				x			
<i>Vitrea subrimata</i>				x			
<i>Semilimax semilimax</i>							x
<i>Perforatella incarnata</i>	x	x			x		
<i>Perforatella bidentata</i>			x		x		
<i>Hygromia limbata</i>	x	x	x	x	x		
<i>Belgrandia marginata</i>	x	x	x		x		
Espèces éteintes							
<i>Retinella (Lyrodiscus) elephantium</i>	x	x	x	x	x	x	x
<i>Succinea joinvillensis</i>		x	x				
<i>Zonitoides sepultus</i>	x	x				x	
<i>Aegopinella bourdieri</i>	x	x	x				
<i>Aegopsis acieformis</i>	x	x	x				
<i>Fruticicola chouquetiana</i>	x		x				



Retinella (Lyrodiscus) elephantium

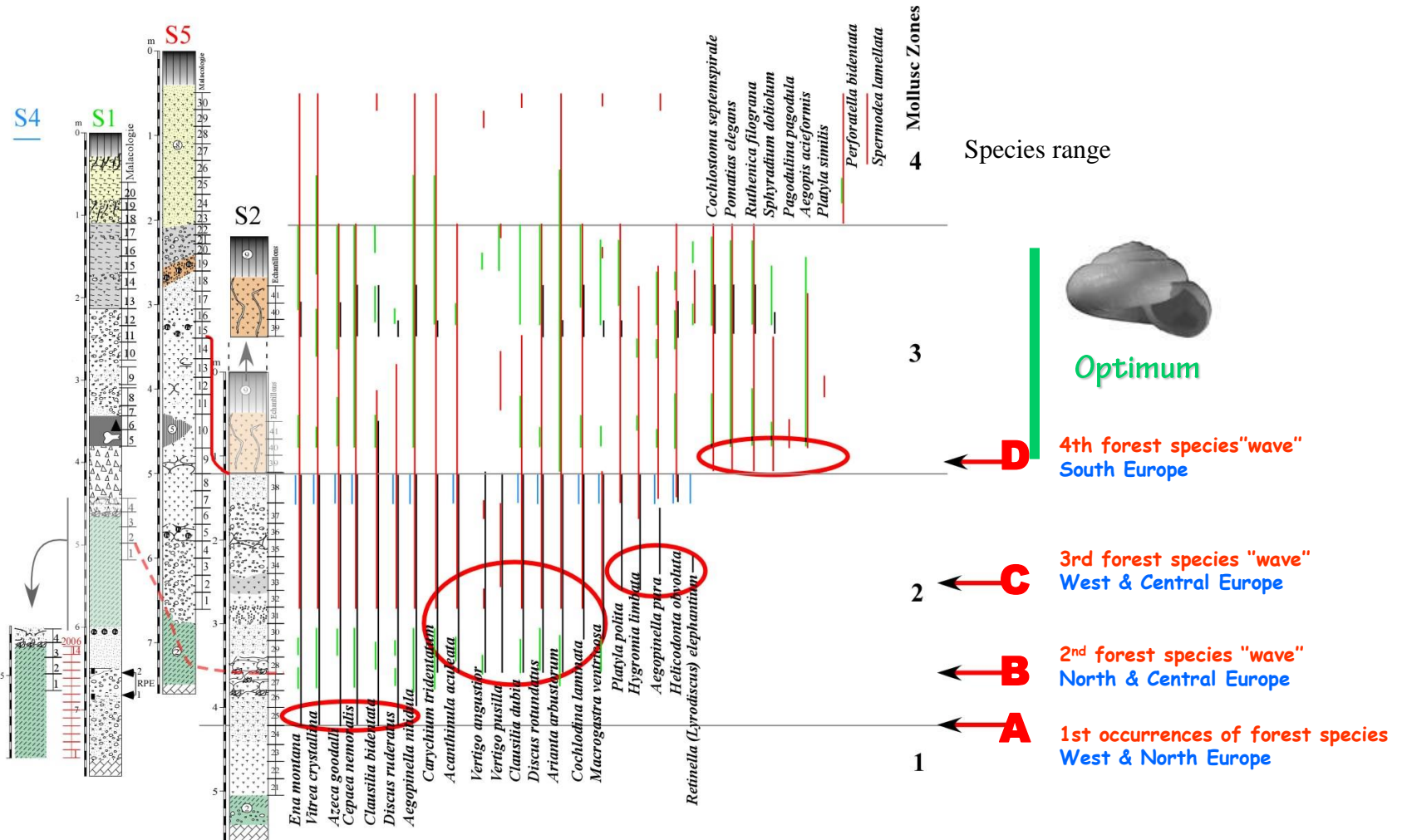


Dense humid forest

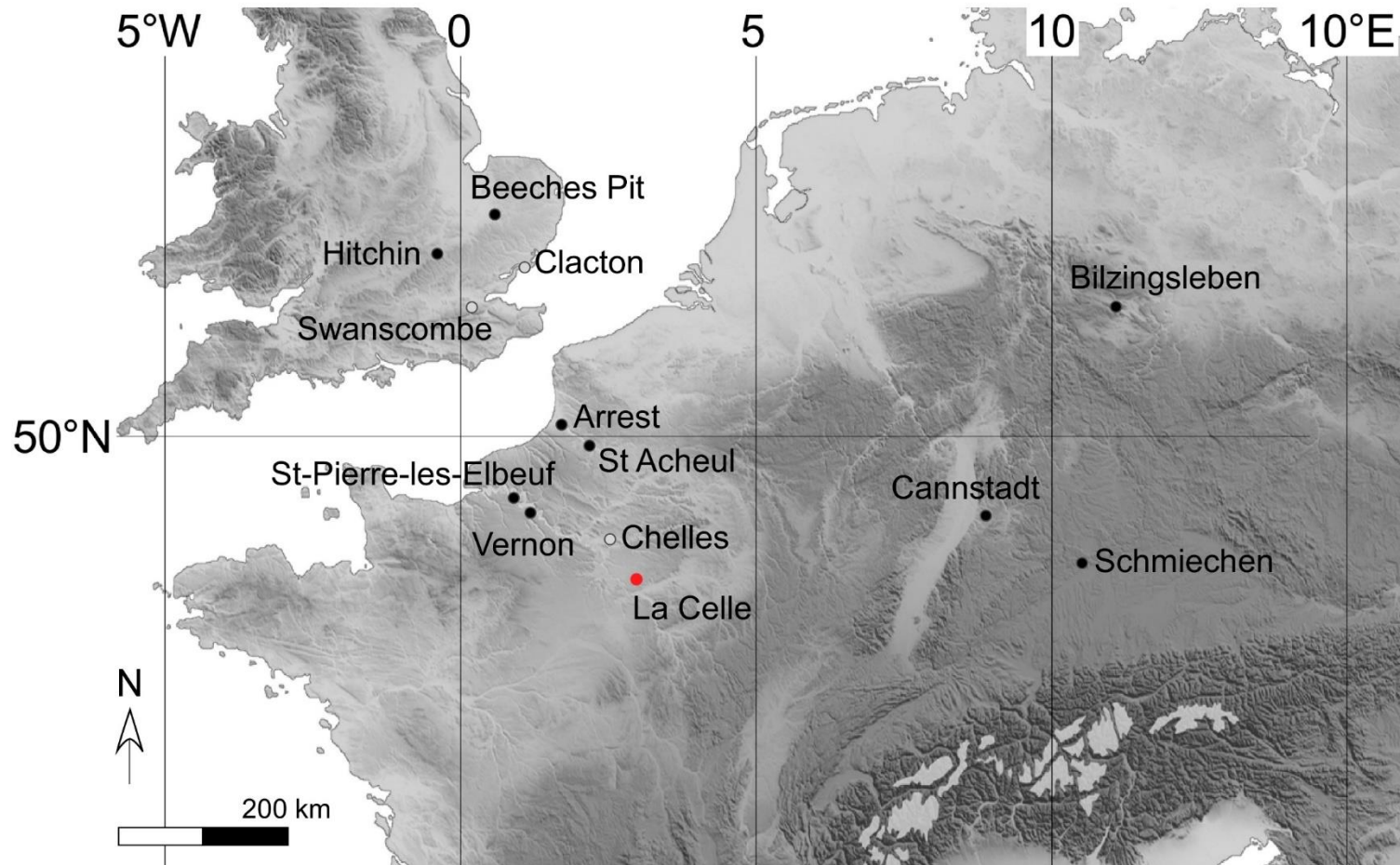


Succession of forest malacological assemblages at La Celle (MIS 11: 400 kyr)

longest and only tufa deposit to yield a detailed record of forest expansion during MIS 11 > regional model

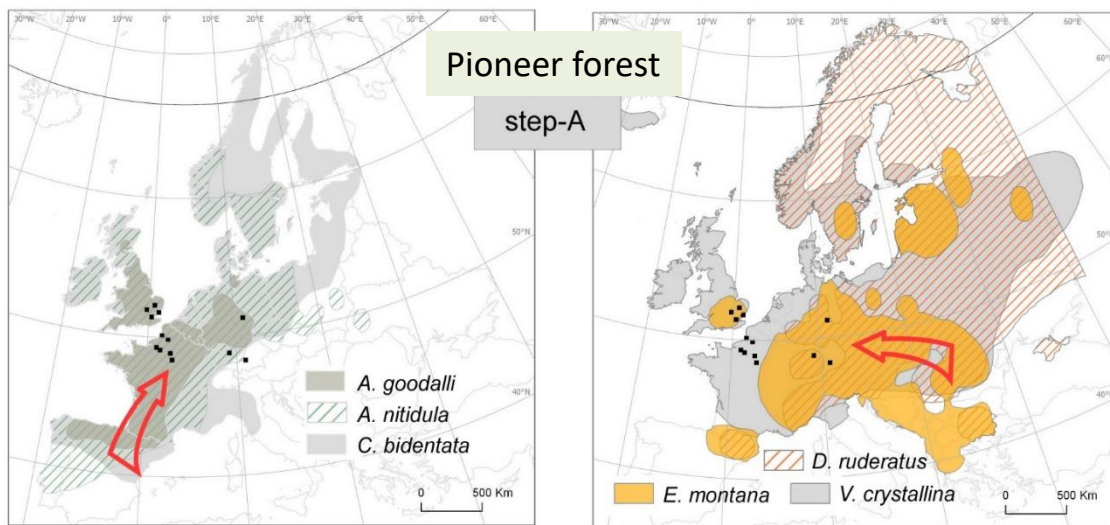


MIS 11 sites with malacological assemblages

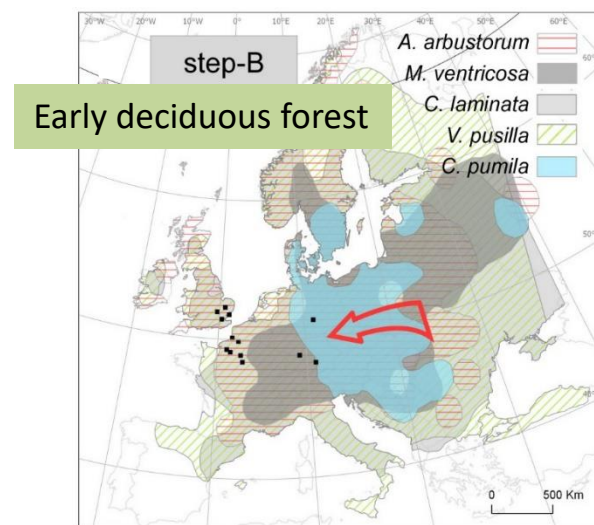


MIS 11 forest species recolonization

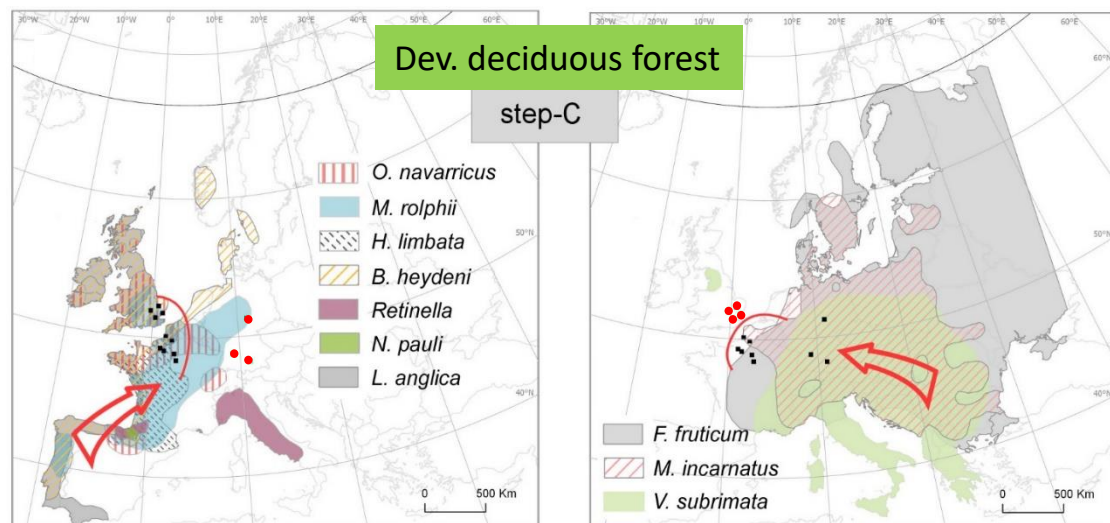
MIS 11 occurrences: presence absence



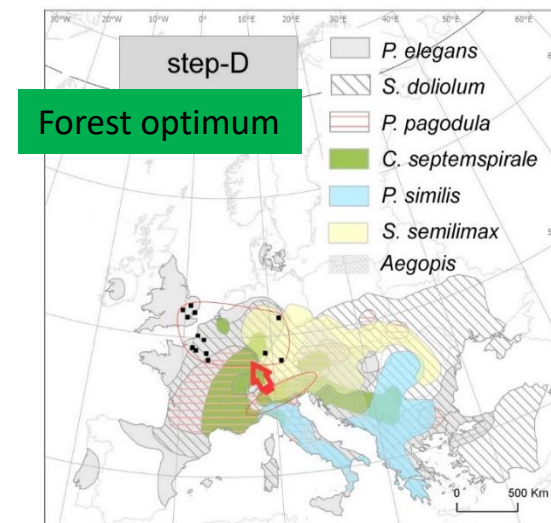
West & North Europe



North & Central Europe



West & Central Europe



South Europe

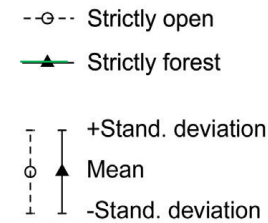
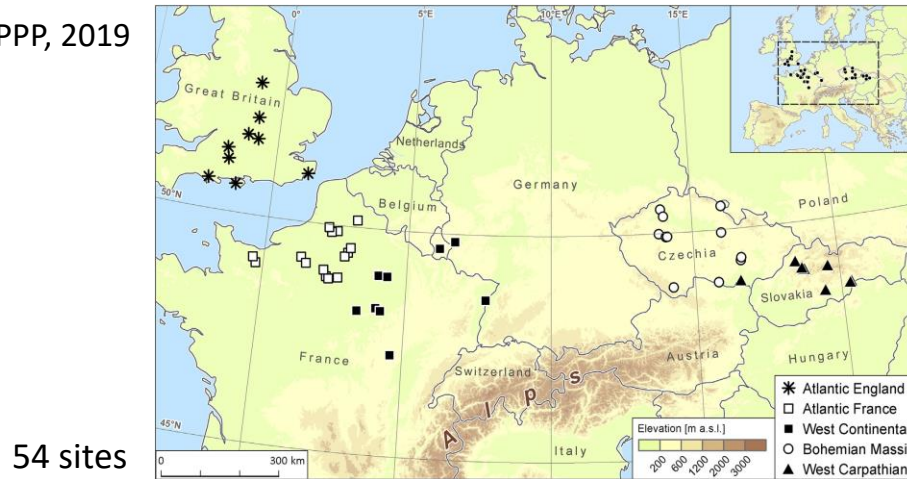
Atlantic and central European refugia = source populations for the recolonization of north-western Europe.
Southernmost taxa reach the area only during the climatic optimum.

The Holocene fauna : Somme basin (North France)

		Species out of range	Species occurring only during the Holocene	
Forest		Discus ruderratus Ena montana	Macrogastera rolphii Acicula fusca Merdigera obscura	TUFA
		Jaminia quadridens Chondrula tridens Vertigo alpestris	Helicella itala Abida secale Monacha cartusiana	FLUVIAL SILTS
Open ground	dry			
	wet	Helicopsis striata Cochicopa nitens Columella columella		

The Holocene: regional variability

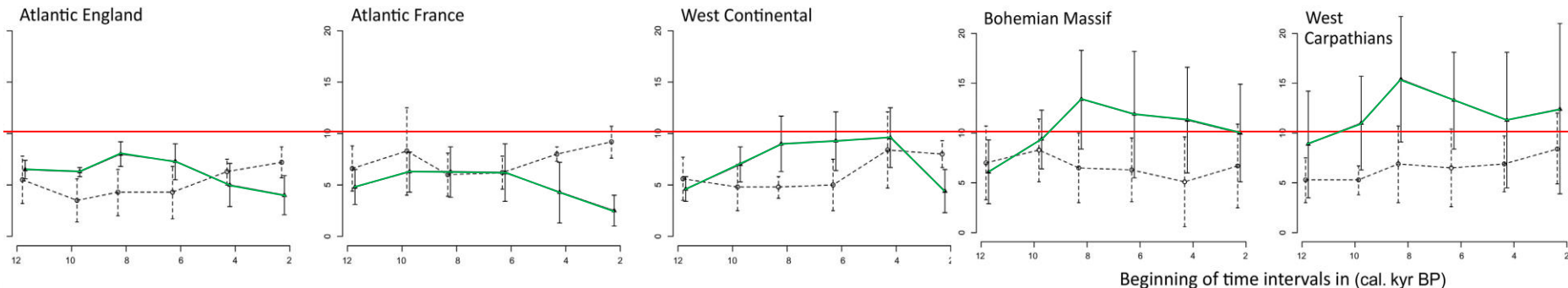
Horsak et al, PPP, 2019



Time intervals (cal. kyr BP):

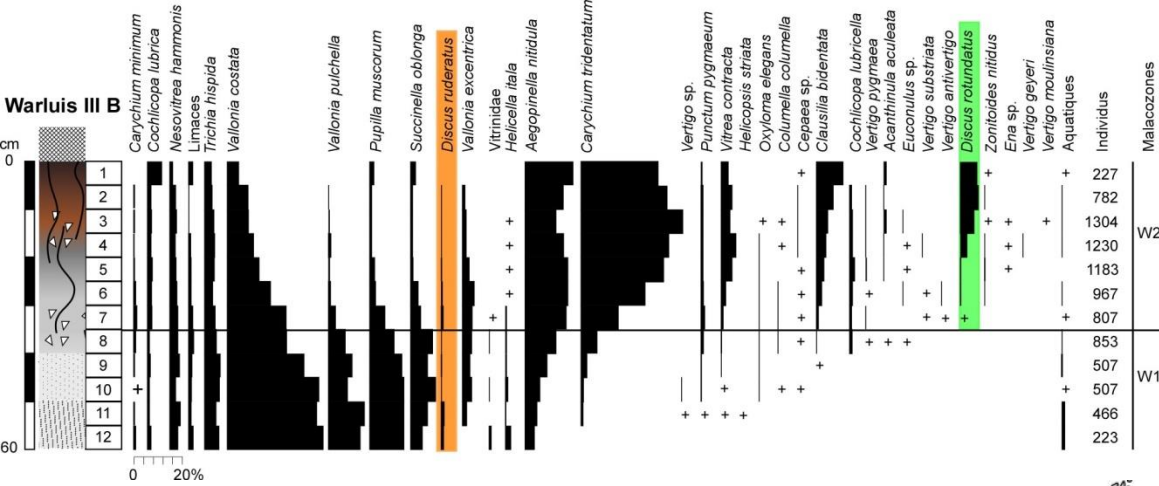
11.7-9.7; **9.7-8.2**; **8.2-6.2**; **4.2-2.2**; **2.2-0.2**
 (beginning of each interval is in bold)

Number of species recorded per sample



East-West gradient in the Holocene dynamic of land snail assemblages, correlating mainly with the changes in strictly forest species richness.

East: glacial refugia in the Carpathian Mountains



The Holocene: Lots of sites + Range of ¹⁴C tracing snails in time



9500 BP

Discus ruderatus

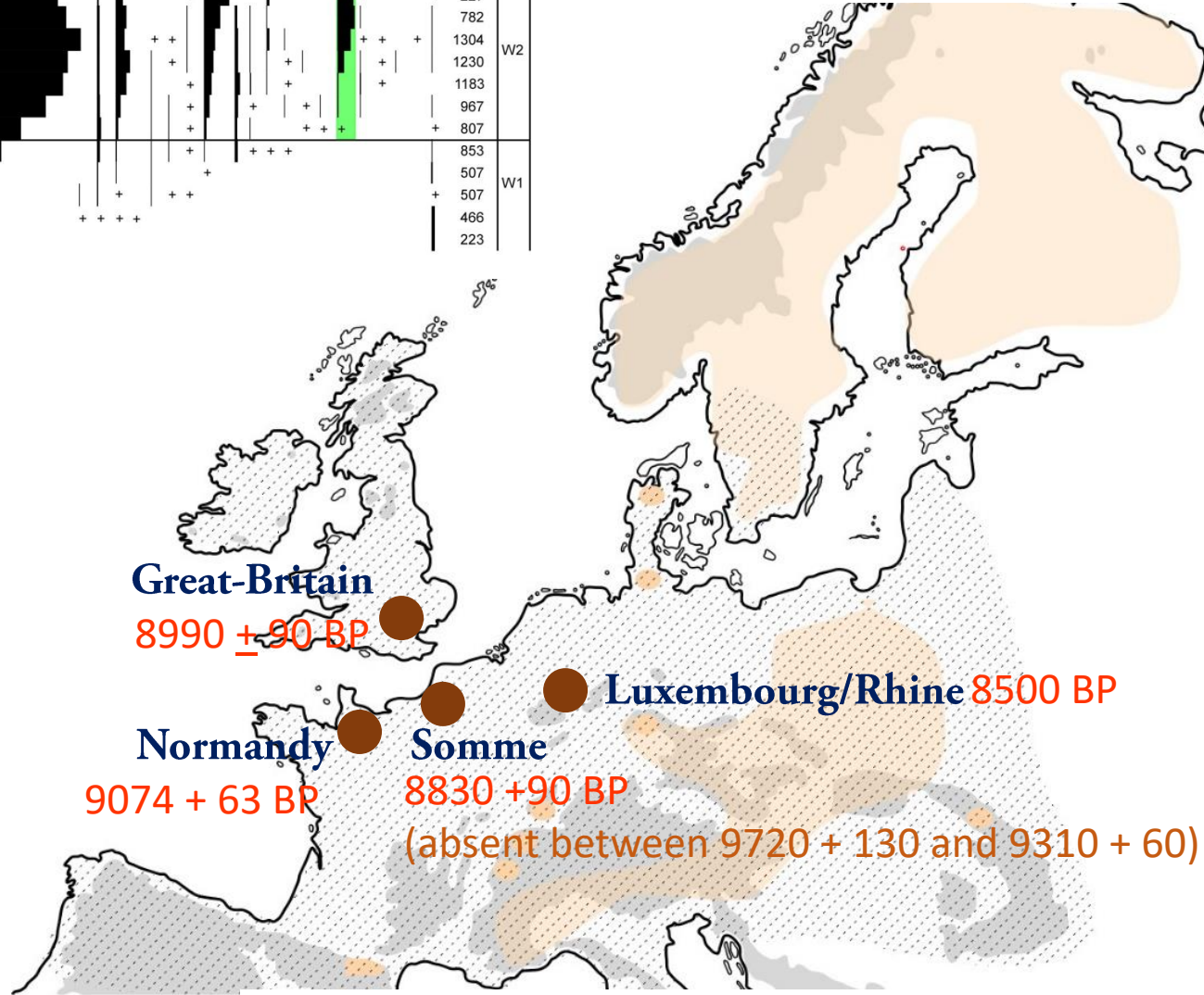
Coniferous woods and moist habitats. Boreal and Alpine (pink).



9000 BP

Discus rotundatus

Deciduous forest, shaded places. Common in Europe (dots) Introduced in South Scandinavia.



Appearance of *Discus rotundatus* within
Holocenes sequences from NW Europe

Interglacial land snails faunas

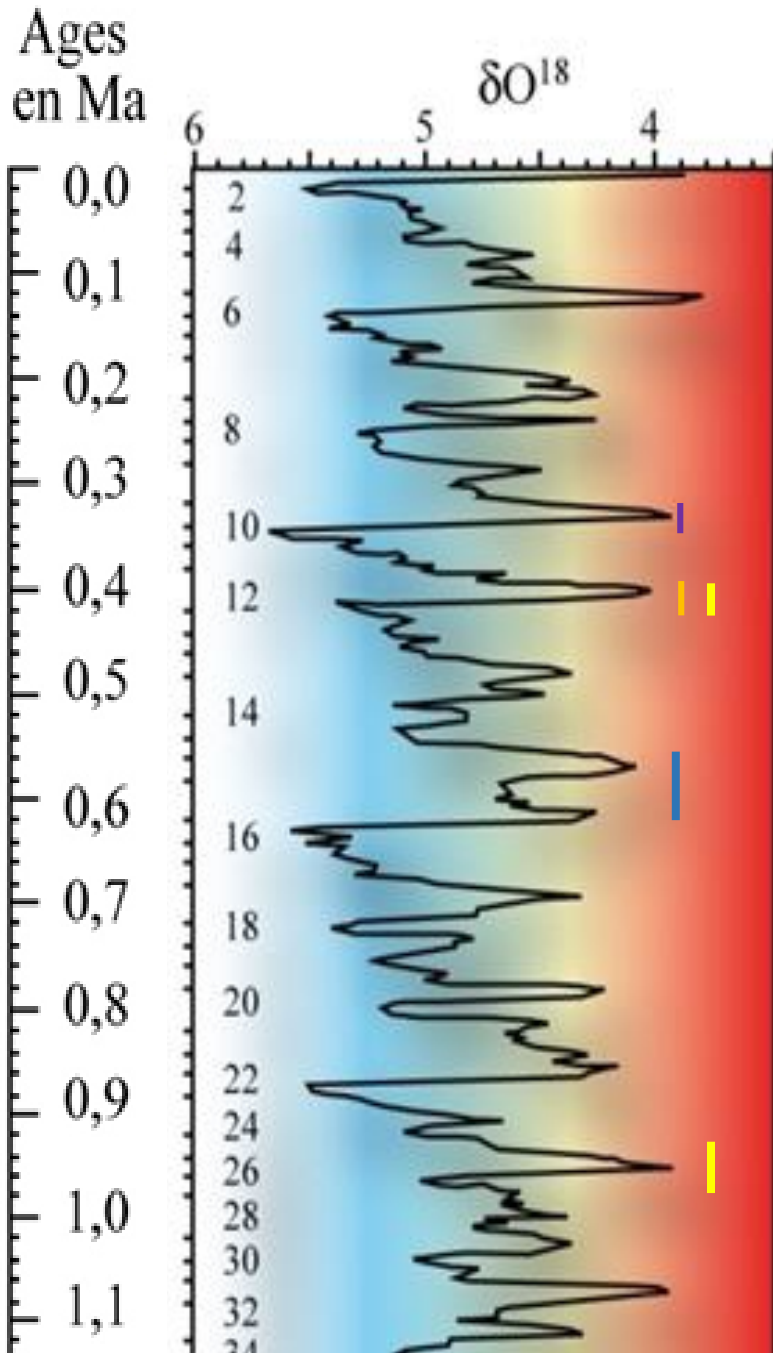
Hotspot of palaeobiodiversity

Humidity is an important driver of malacofaunas diversity

Arrival of species is highly dependent on the distance to the refuge areas and their ecological tolerance.

Many species experienced changes in distribution

Interglacial malacological succession provide good biostratigraphical references



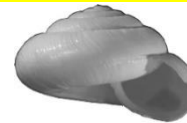
Quaternary extinctions the fragility of thermophiles

No extinctions after MIS 9
(since 200 000 yrs)

Corbicula fluminalis



Retinella (Lyrodiscus) elephantium



5 mm

Candidula radigueli



Tanousia cf. runtoniana



2 mm

Number of extinctions since 1 MA:
4 in the Somme
10 in the Paris basin
8 in UK
13 in total

Current vs. Quaternary fauna

(excluding slugs and sub-species)

Example of the Somme valley: 1 Myr, 34 sites, 300 samples

— aquatics — terrestrial — total



Holocene

Upper Pleistocene

Middle Pleistocene

What are the missing species during the Quaternary?



Species of the present fauna of the Somme that were absent during the Quaternary in Northwestern Europe

Ashfordia granulata (Alder, 1830)
Balea heydeni von Maltzan, 1881
Euconulus praticola (Reinhardt, 1883)
Euconulus trochiformis (Montagu, 1803)
Oxyloma sarsii (Esmark, 1886)
Trochulus sericeus (Draparnaud, 1801)
Trochulus striolatus (C. Pfeiffer, 1828)
Mercuria anatina (Poiret, 1801)
Stagnicola fuscus (C. Pfeiffer, 1821)
Euglesa globularis (Clessin, 1873)
Sphaerium nucleus (S. Studer, 1820)
Sphaerium ovale (Férussac, 1807)
Unio crassus Philipsson, 1788

25 species

Pb of identification and conservation

12 species

 *Pseudotrichia rubiginosa* (Rossmässler, 1838)
Marstoniopsis insubrica (Küster, 1853)
Cerneuella aginnica (Locard, 1882)
Cerneuella neglecta (Draparnaud, 1805)
Hygromia cinctella (Draparnaud, 1801)
Trochoidea elegans (Gmelin, 1791)
Ferrissia californica (Rowell, 1863)
Theba pisana (O.F. Müller, 1774)
 *Potamopyrgus antipodarum* (Gray, 1843)
Corbicula fluminalis (O.F. Müller, 1774)
Corbicula fluminea (O.F. Müller, 1774)
Dreissena polymorpha (Pallas, 1771)

Favoured area extensions(6)

Proven introductions (6)

CLIMATE

From 1 MA to 200 Kyr (8000 c) = 4 extinctions

Since 400 Ka (4000 c) = 36 area variations = 1/11.000 yrs or 0,009/century

or

Over the last 5 ITGL 88 Kyr (880 c) = 29 area variations = 1/3000 yrs or 0,33/century

Forest species

ANTHROPIISATION

Last 2 centuries = 12 area variations = 1/16 yrs or 6/century

Xerophilous and aquatic species



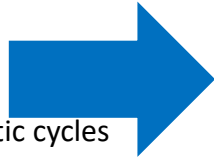
18 times greater than during past interglacials

Conclusions

Palaeobiodiversity

Evolution of richness over climatic cycles

Climatic and anthropogenic impact



Rhythm of recolonization

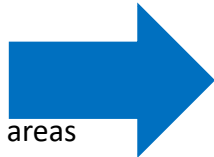
Pleistocene Itgl forest faunas richer than the Holocene

Anthropogenic impact favour introduction of xerophilous and aquatic molluscs

Palaeobiogeography

Changes in species distribution areas

Understanding current distribution



Many changes in species distribution during past Itgl > question current « endemics » > mainly forest snails

Modern rhythm of changes in species distribution increase dramatically > mainly xerophilous and aquatic molluscs

Palaeoecology

Variation in species tolerance to habitat modification

Main parameters driving mollusc development



Ecological requirements of species remain stable except a few opportunistic behaviour during periods of rapid climatic oscillation

Recolonization driven by:

Temperature + Humidity + distance of refuge areas
> Habitat fragmentation vs restoration program



Thanks for your attention

