Applications of P systems in population biology and ecology

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joint work with
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Population modelling: motivations

- Models contribute to understanding the factors governing population growth, evolution, extinction, …
  - Hypothesis validation
- Models allow making predictions on the future of a population of interest
  - e.g. endangered species
- Models can support decision making in planning control policies
  - e.g. reintroduction actions

Population modelling: application domains

- Population biology
  - causes of extinction of species, demography, …
- Ecology
  - sustainable development, biodiversity, …
- Evolutionary biology
  - species formation, …
- Social sciences
  - social behaviours, animal sociology, …
- Epidemiology
  - spread of diseases, role of vaccination, ...

Population modelling: traditional methodologies

- Mathematical modelling (ODEs, recurrence eq., …)
  - e.g. Lotka-Volterra predator-prey equations
  - e.g. Susceptible/Infective/Recovered (SIR) epidemic model
  - **Problems:** unfriendly notation, deterministic dynamics
- Agent based modelling
  - Individuals models as agents whose behaviour is described by an algorithm or set of rules
  - Probably the most used methodology in ecological modelling (*Individual Based Modelling – IBM*)
  - **Problems:** often unformalized/ambiguous

Population modelling: P systems

- P systems can provide a simple, elegant and unambiguous notation for population modelling
- **Objects** can represent
  - individuals (and their current state)
  - available natural resources (e.g. food)
  - state of the environment (e.g. season, weather)
- **Evolution rules** can represent events like
  - birth, mating, oviposition, growth, death, predation, transmission of diseases, fight, communication, aggression, …

Population modelling: P systems

- Maximal parallelism is good for modelling populations that evolve by stages
  - All the individuals are involved in the same activity (e.g. reproduction season, hibernation, …)
- Particularly useful if combined with rule promoters
  - to enable different rules during different stages
- But also probabilities are necessary
  - sometimes individuals can be subject to alternative events (e.g. birth of male/female), or can make choices
  - in particular when the population size can be small

Minimal Probabilistic P systems

- These observations led us to the definition of Minimal Probabilistic P systems (MPP systems)
- They are P systems based on

Probabilistic maximal parallelism

with rule promoters

- They are minimal in the sense that we tried to include as less features as possible…
- No membrane structure…

Minimal Probabilistic P systems

MPP system A *Minimal Probabilistic P system* is a tuple $\langle V, w_0, R \rangle$ where:

- V is a possibily infinite alphabet of objects, with V^* denoting the universe of all multisets having V as support.

- $w_0 \in V^*$ is a multiset describing the initial state of the system

- R is a finite set of evolution rules having the form

$$u \xrightarrow{f} v \mid_p$$

where $u, v, p \in V^*$ are multisets (often denoted without brackets) of *reactants*, *products* and *promoters*, respectively, and $f : V^* \mapsto \mathbb{R}^{\geq 0}$ is a *rate function*.

Probabilistic maximal parallelism

Briefly: pick rules one-by-one with probabilities proportional to their rates until you get a maximal multiset of rule instances

Algorithm 1 Probabilistic maximally parallel evolution step

function $\textsc{Step}(w)$

  $x = w$

  $y = \emptyset$

  while there exists $u \xrightarrow{f} v \mid_p$ in R s.t. $u \subseteq x$ and $p \subseteq w$ **do**

    $R' = \{u \xrightarrow{f} v \mid_p \in R \mid u \subseteq x \text{ and } p \subseteq w\}$

    choose $u' \xrightarrow{f'} v' \mid_{p'}$ from R' with a probability proportional to $f'(w)$

    $x = x \setminus u'$

    $y = y \cup v'$

  end while

  return $x \cup y$

end function

Probabilistic maximal parallelism

- In the end, probabilistic maximal parallelism turns out to use probabilities just to choose among rules that compete for the same objects
- An applicable rule that does not compete with any other rule will be for sure applied, whatever its rate is
- **Note:** applicable rules should always have a positive rate

Analysis techniques

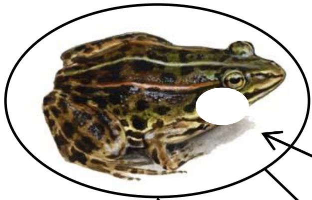
- Simulation
- Statistical model checking:
  - The analysis technique we choose (and suggest) for population and ecosystem modelling
  - A statistical model checker:
    1. runs a number of simulations of the model of interest
    2. use simulation results (execution traces) to construct a Discrete Time Markov Chain representing the system behaviours
    3. verifies behavioural properties (expressed as temporal logic formulas) on the Markov Chain (model checking)
  - We defined the translation of MPP systems into the PRISM (model checker) input language

Application: hybrid populations of water frogs

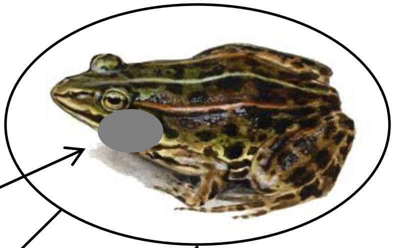
- We applied MPP systems to investigate an **open problem** in evolutionary biology:
  - To understand the mechanisms underlying the stability of European hybrid populations of water frogs

Among European water frogs there are two species …

Pelophilax lessonae



Pelophilax ridibundus



Differences

Vocal sacs

Size

Adapted to mashes and ponds
Pool frogs

Adapted to lakes
Lake frogs

which interbred producing hybrids with intermediate characteristics

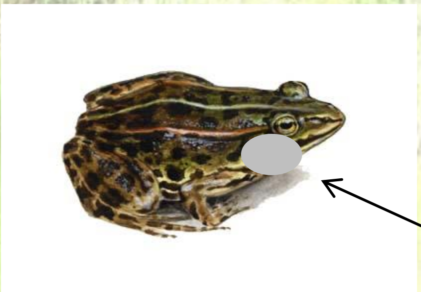
Pelophilax lessonae

Pelophilax ridibundus

male

female

Edible frogs

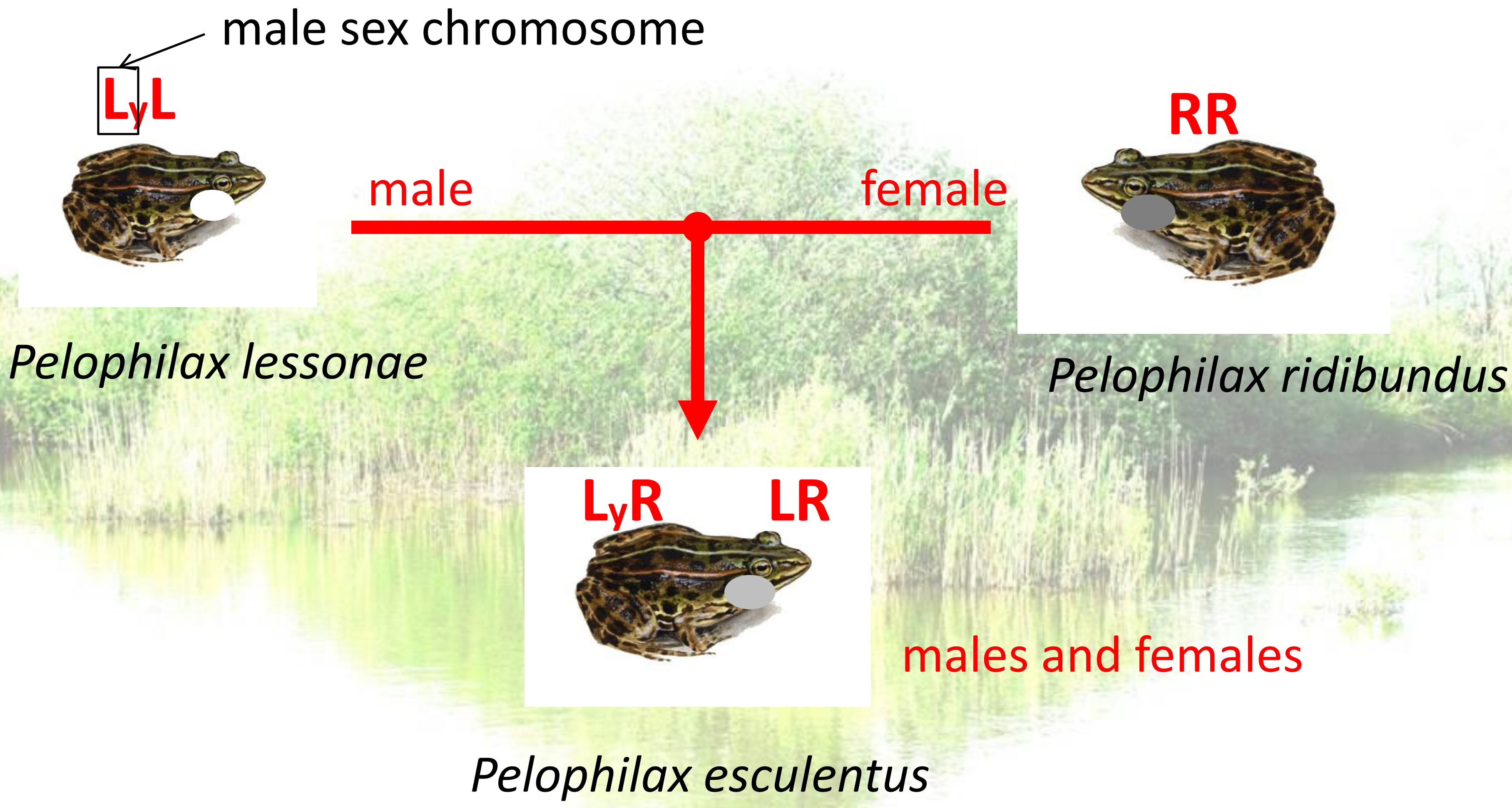


Pelophilax esculentus

light grey
intermediate size

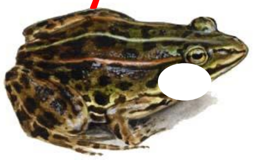
Note: for size reasons the interbreeding involves *P. lessonae* males and *P. ridibundus* females

Some notation



P. ridibundus are currently limited to Eastern Europe

L_yL



LL

Pelophilax lessonae

L_yR

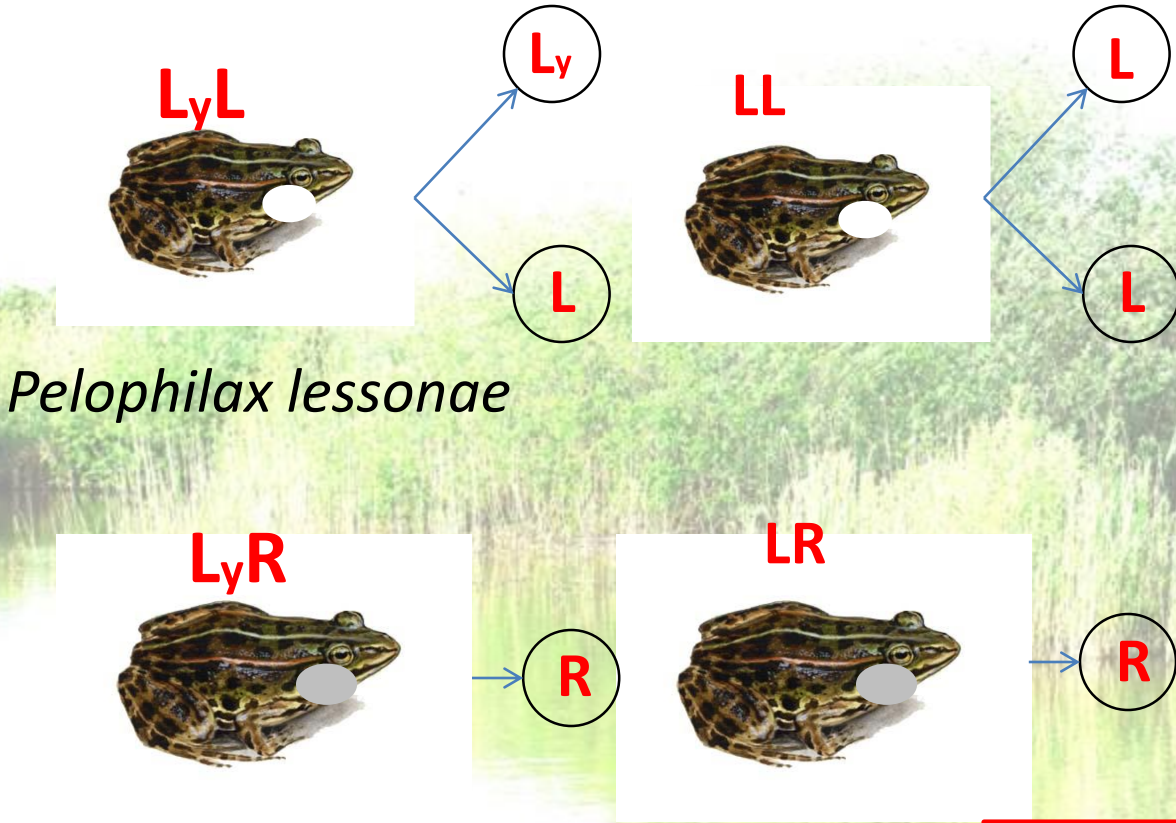
LR

Pelophilax esculentus

In Western Europe are diffused populations of coexisting *P. lessonae* and *P. Esculentus*

L-E complexes

P. esculentus have a particular gametogenesis (hemiclonal)



Pelophilax esculentus

Hemiclonality: there is no recombination between chromosomes

Resulting in the following reproduction table

LL

LR

L_yL

L_yR

	LL	LR
L_yL	L_yL LL	L_yR LR
L_yR	LR	RR

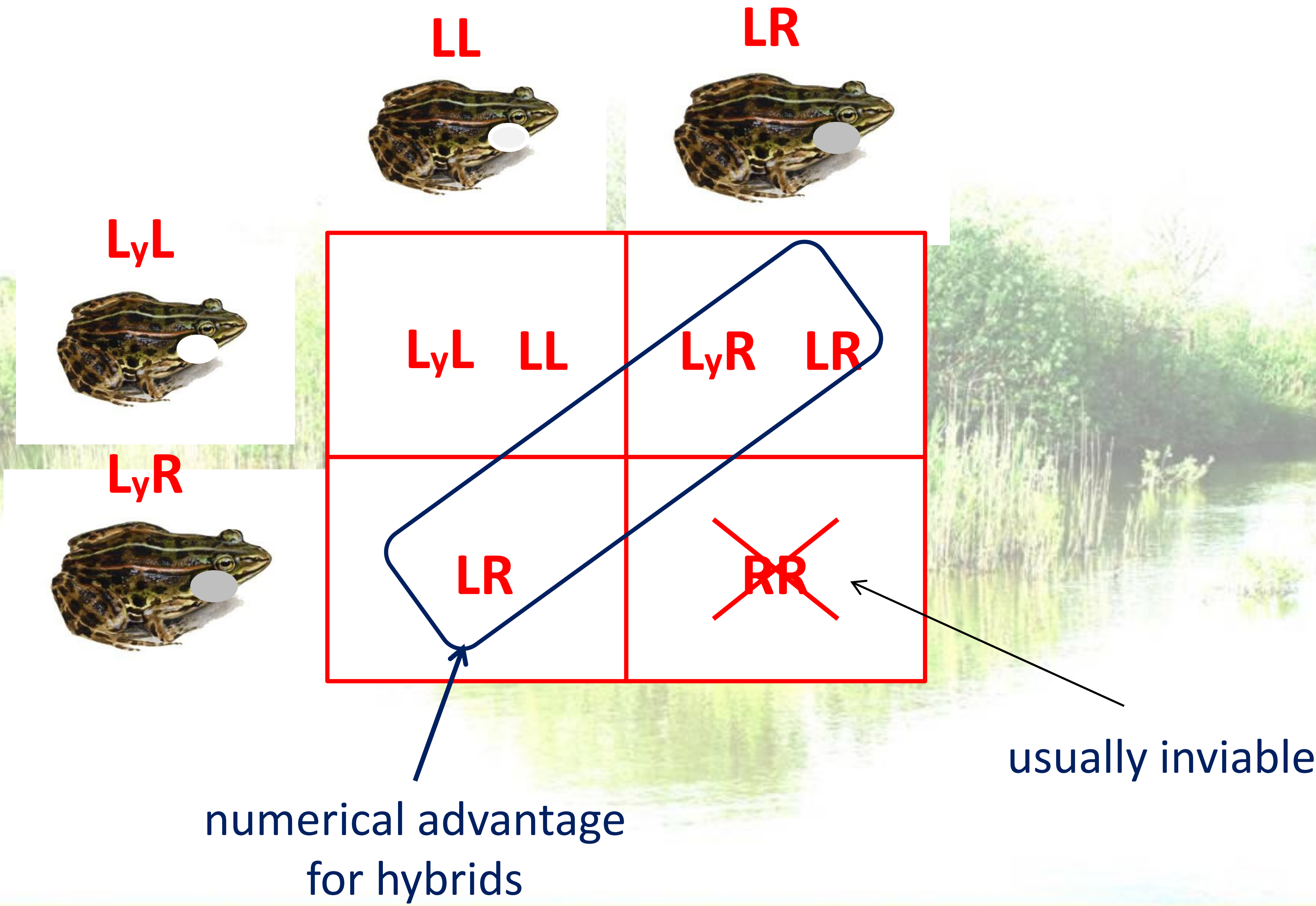
Resulting in the following reproduction table




	LL	LR
L_yL	L_yL LL	L_yR LR
L_yR	LR	~~RR~~

usually inviable

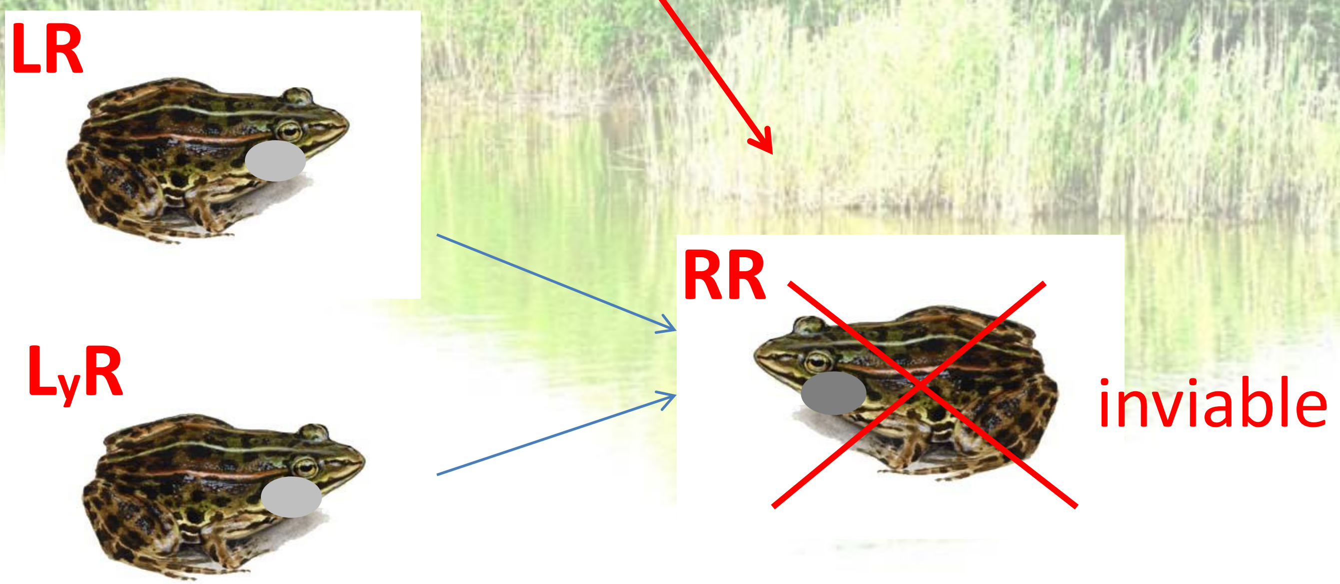
Resulting in the following reproduction table



Consequences:

- Hybrids are numerically advantaged
- Hybrids show heterosis (hybrid vigor)

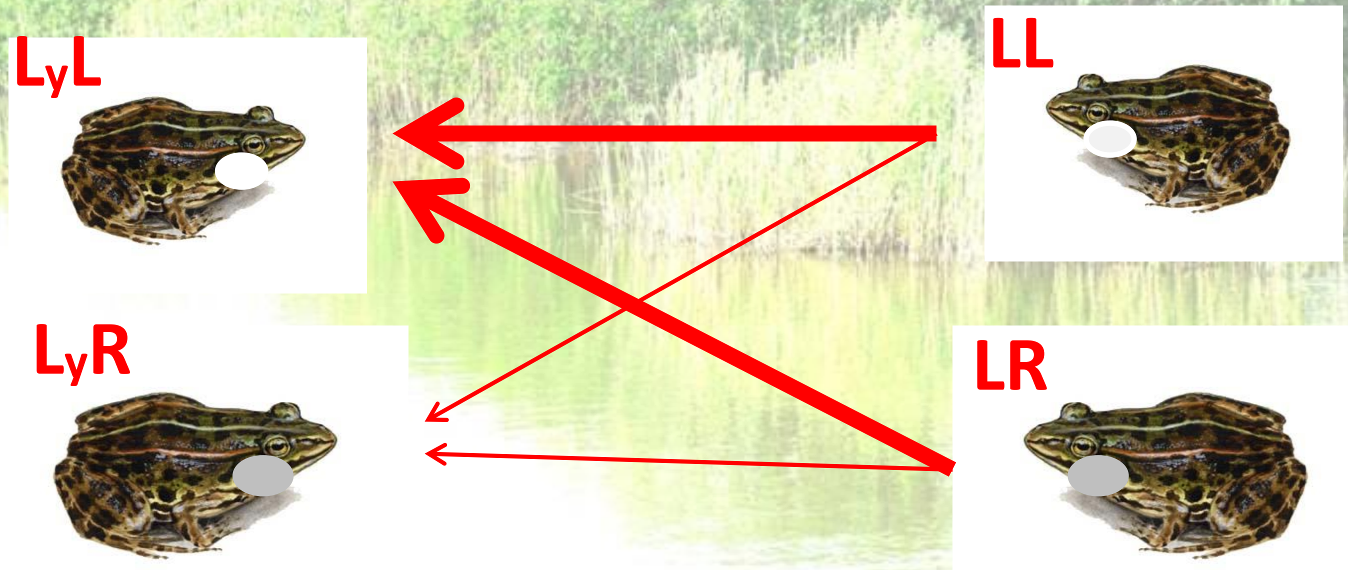
They should outcompete the parent species (*P. lessonae*), but *P. esculentus* alone cannot survive!!
(they can survive only as reproductive parasites)



How can L-E complexes not to get extinct?
An answer based on observations and experiments:

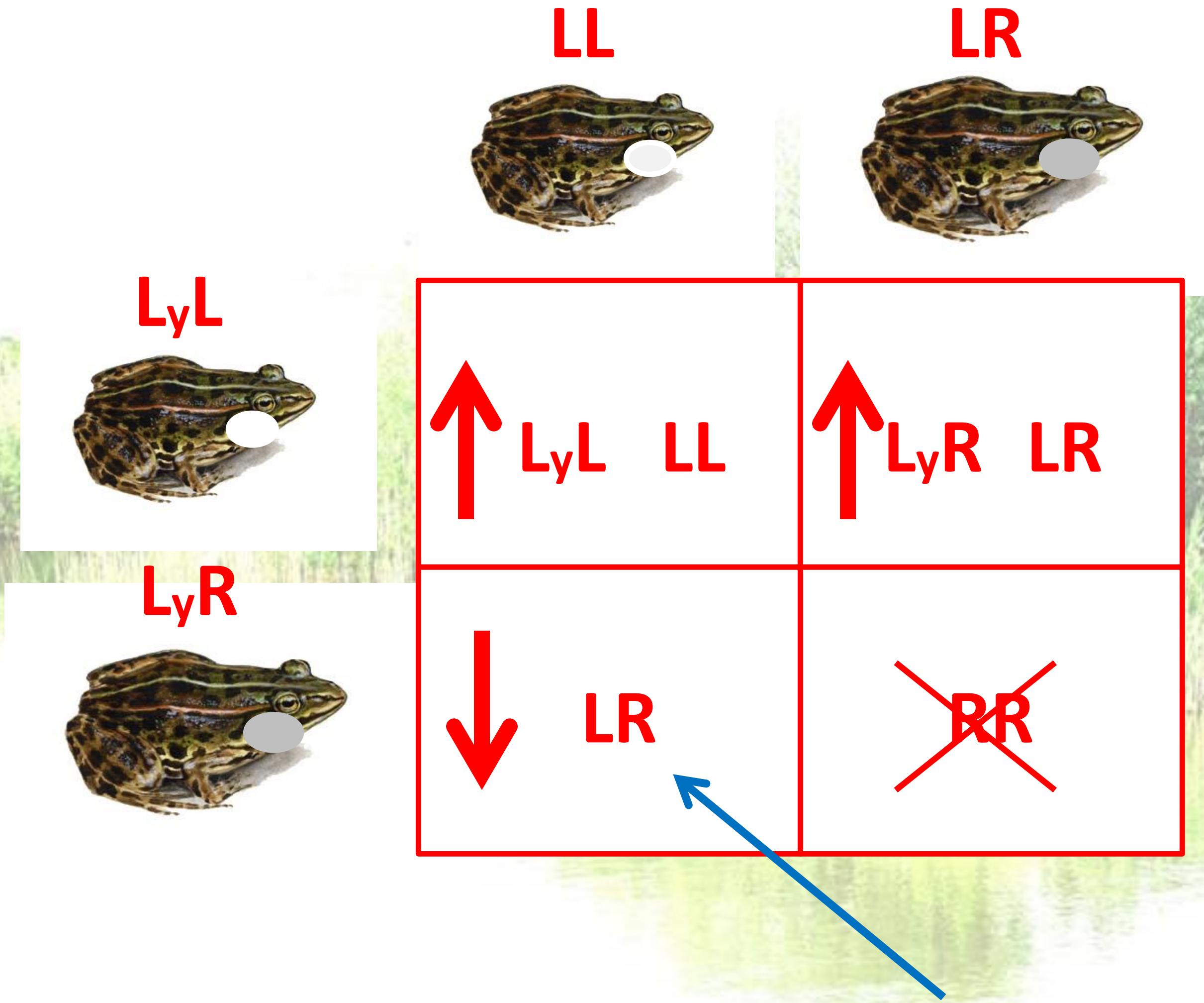
female sexual preferences

In water frogs females are choosy and males are promiscuous



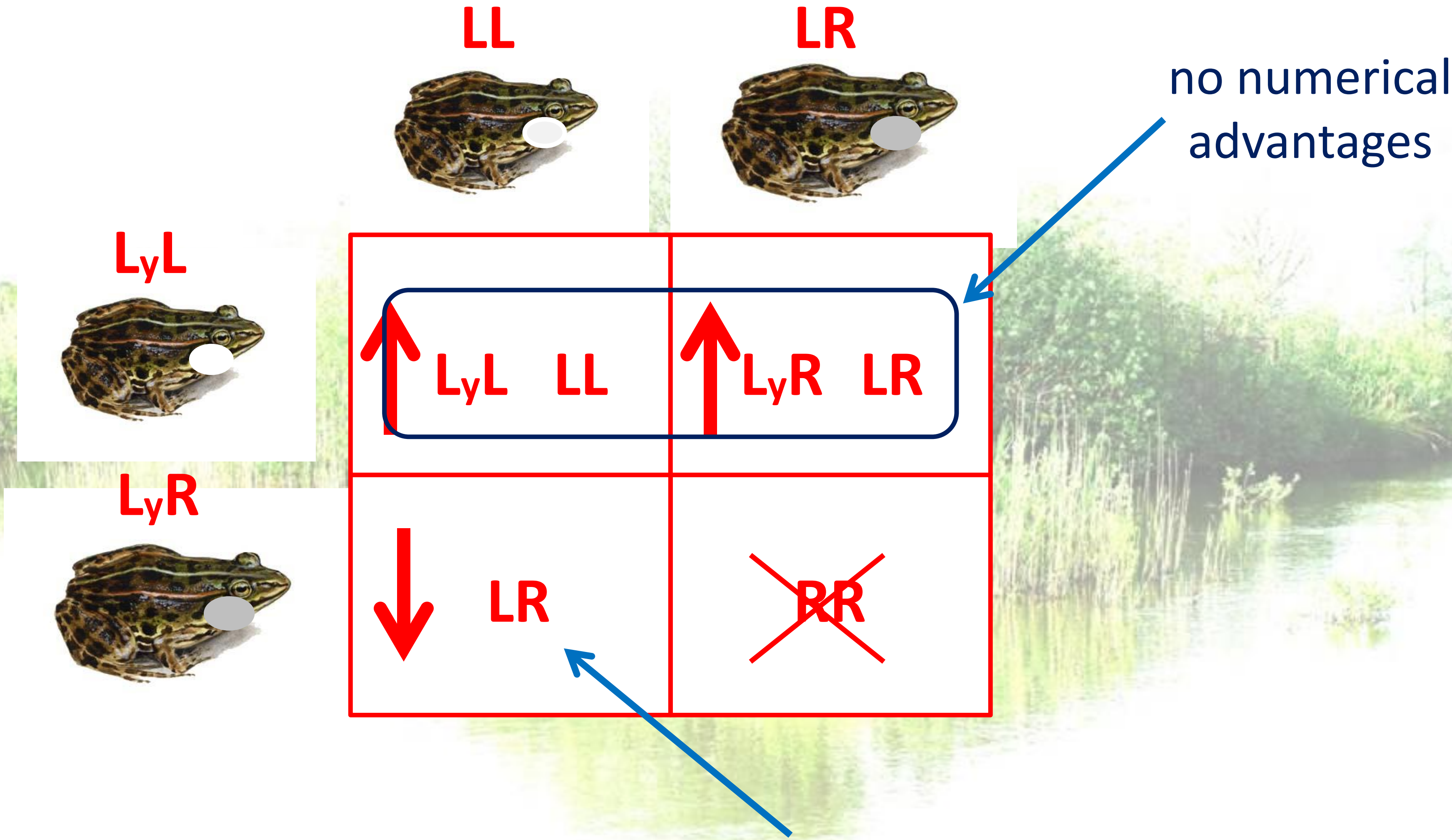
females of both species prefer *P. lessonae* males

Consequence of female preferences:



if female preferences are strong enough this entry is negligible

Consequence of female preferences:



if female preferences are strong enough this entry is negligible

Why *P. ridibundus* are not viable?

- The R genome is transmitted clonally, without any recombination, thus:
  - accumulated deleterious mutations cannot be purged
  - this phenomenon is known as “Muller’s ratchet”.

In hybrids the dysfunctionalities of the R genome are compensated by the L genome

L-E complexes: MPP systems model

The model of L-E complexes is the MPP systems $\langle V_{LE}, w_{0LE}, R_{LE} \rangle$

where $V_{LE} = V_{LEa} \cup V_{LEj} \cup V_{ctrl}$

with

$$V_{LEa} = \{ LL \,,\, L_yL \,,\, LR_* \,,\, L_yR_* \,,\, LR_\circ \,,\, L_yR_\circ \,,\, R_*R_\circ \,,\, R_\circ R_\circ \}$$

$$V_{LEj} = \{ LL^j \,,\, L_yL^j \,,\, LR_*^j \,,\, L_yR_*^j \,,\, LR_\circ^j \,,\, L_yR_\circ^j \,,\, R_*R_*^j \,,\, R_*R_\circ^j \,,\, R_\circ R_\circ^j \}$$

$$V_{ctrl} = \mathbb{N} \cup \{ REPR \,,\, SEL \}$$

L-E complexes: MPP systems model

Evolution rules:

REPRODUCTION

For each kind of male *x*, female *y* and juvenile *z*:

$$x \; y \xrightarrow{f_{xy}} x \; y \; z \;\big|_{REPR}$$

where:

$$f_{xy}(w) = k_{mate}(x, y) \cdot |w|_x \cdot |w|_y \cdot 1/k_{o\_kind}(x, y)$$

L-E complexes: MPP systems model

Evolution rules:

SELECTION (AND GROWTH)

For each kind of individual x and juvenile x^j:

$$x \xrightarrow{g_x} x \,|_{SEL} \qquad x \xrightarrow{g'_x} \epsilon \,|_{SEL}$$

$$x^j \xrightarrow{g_{xj}} x \,|_{SEL} \qquad x^j \xrightarrow{g'_{xj}} \epsilon \,|_{SEL}$$

where:

$$g_x(w) = \frac{1}{\sigma + \frac{|w|}{k_{fit}(x)\cdot cc}} \qquad g'_x(w) = 1 - g_x(w)$$

L-E complexes: MPP systems model

Evolution rules:

STAGES ALTERNATION

$$REPR\ 1 \rightarrow REPR\ 2 \qquad REPR\ 2 \rightarrow REPR\ 3$$

$$REPR\ 3 \rightarrow SEL \qquad SEL \rightarrow REPR\ 1$$

In the end, the model description is rather compact…

$$x\ y \xrightarrow{f_{xy}} x\ y\ z\ |_{REPR}$$

$$x \xrightarrow{g_x} x\ |_{SEL} \qquad x \xrightarrow{g'_x} \epsilon\ |_{SEL}$$

$$x^j \xrightarrow{g_{xj}} x\ |_{SEL} \qquad x^j \xrightarrow{g'_{xj}} \epsilon\ |_{SEL}$$

$$REPR\ 1 \to REPR\ 2 \qquad REPR\ 2 \to REPR\ 3$$

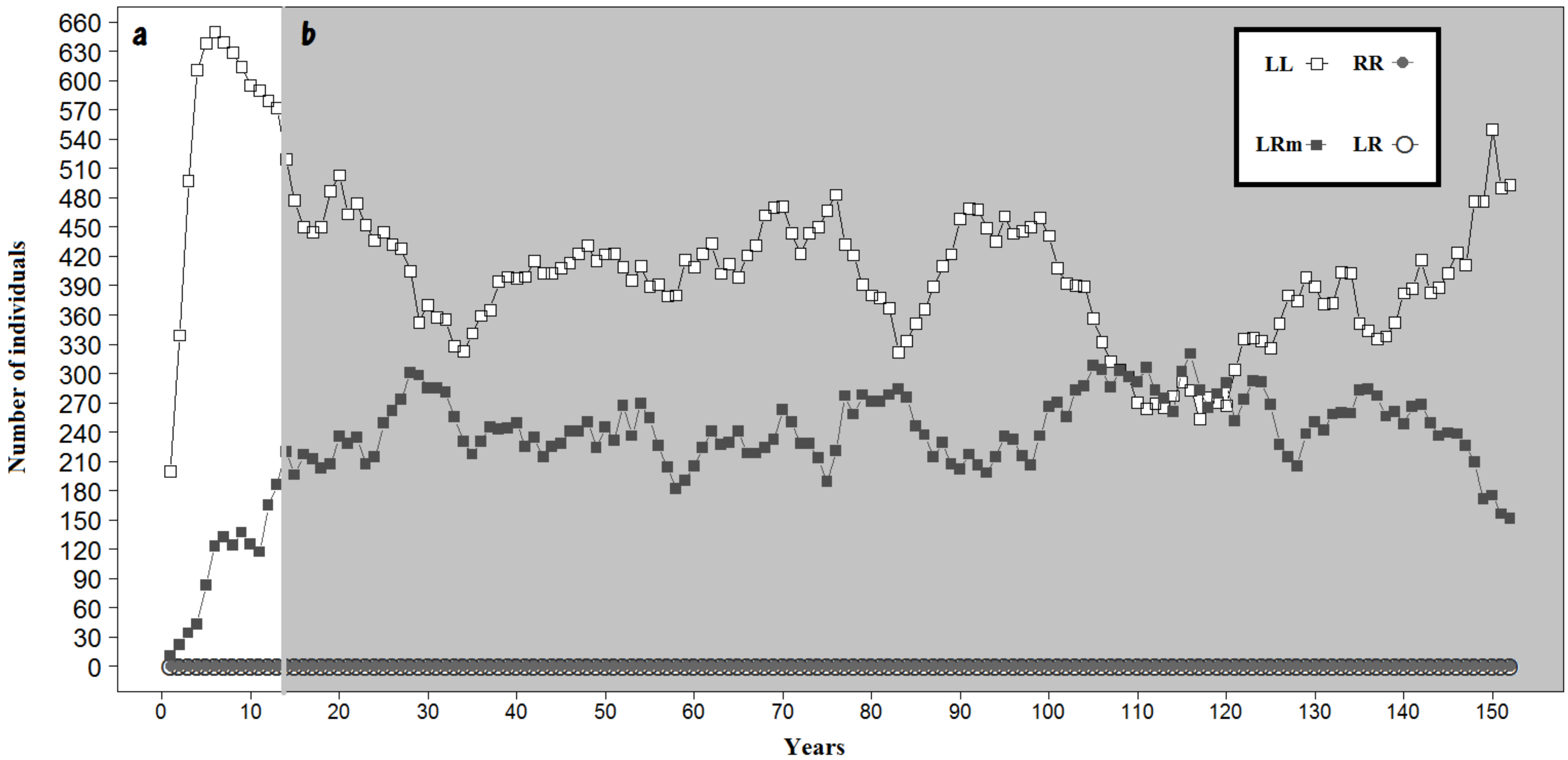
$$REPR\ 3 \to SEL \qquad SEL \to REPR\ 1$$

$$f_{xy}(w) = k_{mate}(x,y) \cdot |w|_x \cdot |w|_y \cdot 1/k_{o\_kind}(x,y)$$

$$g_x(w) = \frac{1}{\sigma + \frac{|w|}{k_{fit}(x)\cdot cc}} \qquad g'_x(w) = 1 - g_x(w)$$

Dynamics of a L-E complex (simulation)

- all R genomes have deleterious mutations
- the sexual preference for *P. lessonae* males is twice than that for *P. esculentus* males
- initial population: 95% of *P. lessonae* and 5% of *P. esculentus*



Probability of extinction

- Statistical model checking (1000 simulations)
- Probability of extinction in 60 years

```
P=?[F total_population=0 & years_counter<=60]
```

- Result: **0.01**

What happens if *P. ridibundus* are viable?

LL

LR

RR

only females

L_yL

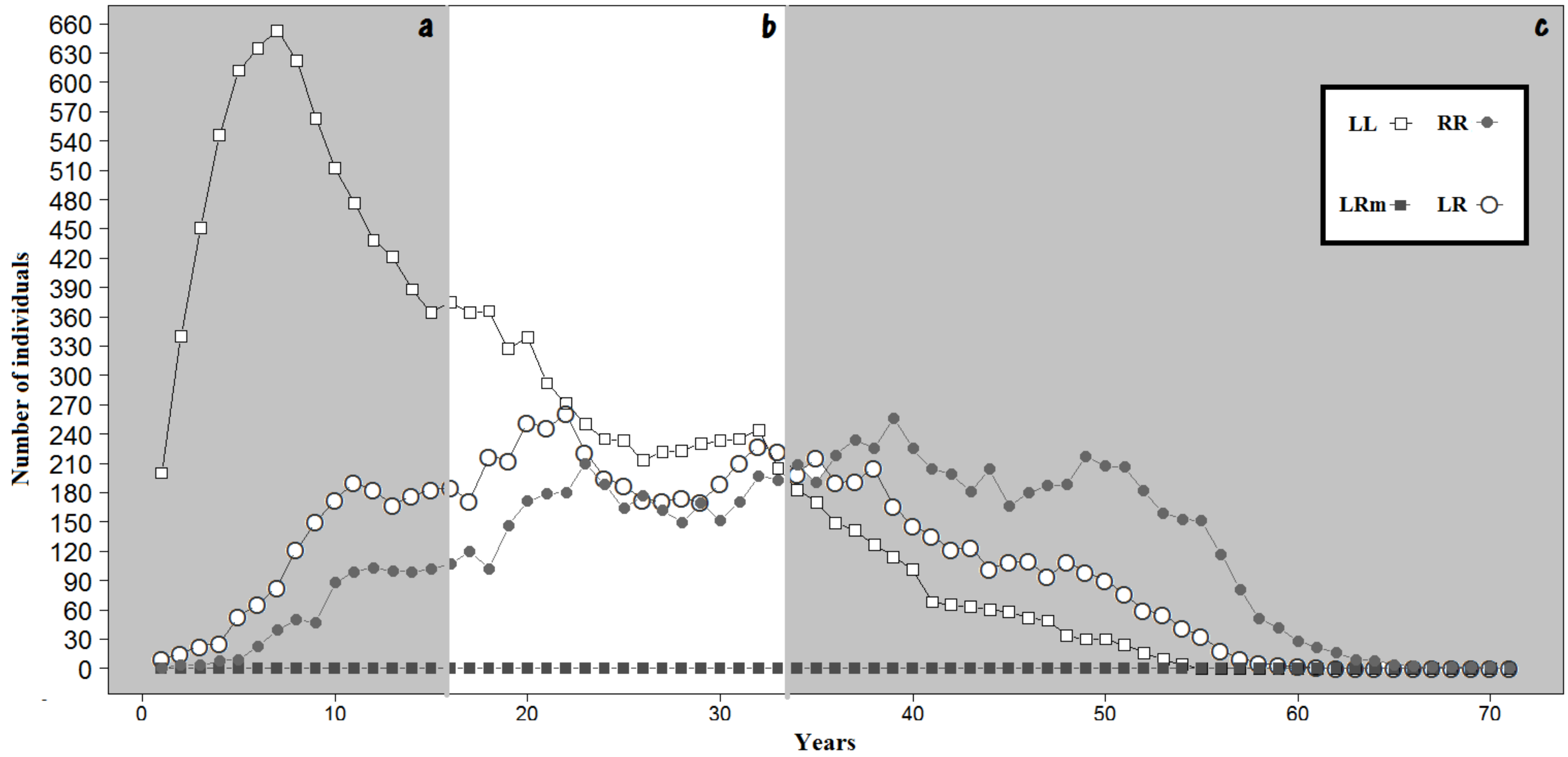
L_yR

	LL	LR	RR
L_yL	L_yL LL	L_yR LR	L_yR LR
L_yR	LR	RR	RR

The number of *P. esculentus* increases. P. lessonae decrease until their extintion. *P. esculentus* and *P. ridibundus* (females) cannot survive: they produce only *P. ridibundus* females.

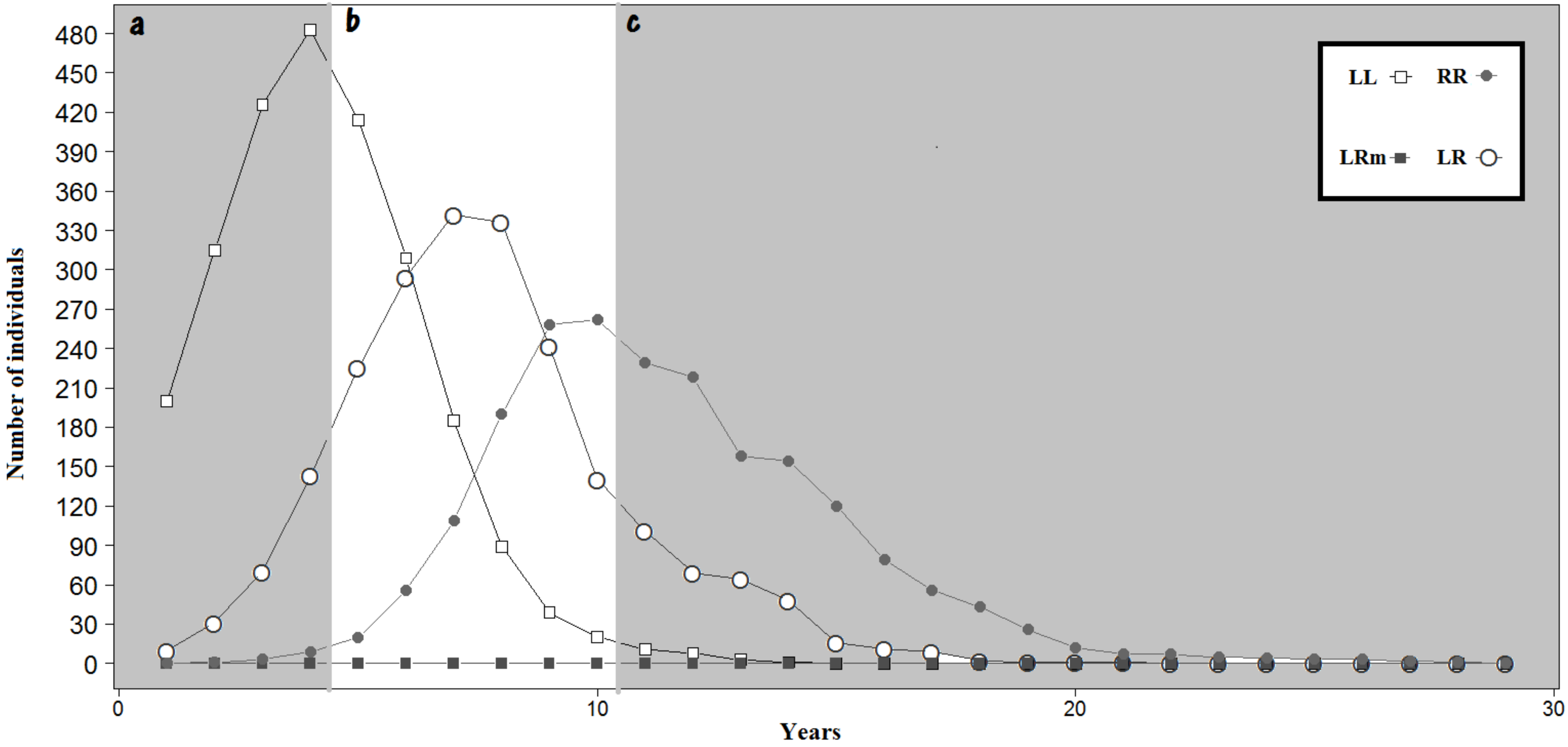
Dynamics of a L-E complex (simulation)

- all R genomes are mutation-free
- the sexual preference for *P. lessonae* males is twice than that for *P. esculentus* males
- initial population: 95% of *P. lessonae* and 5% of *P. esculentus*

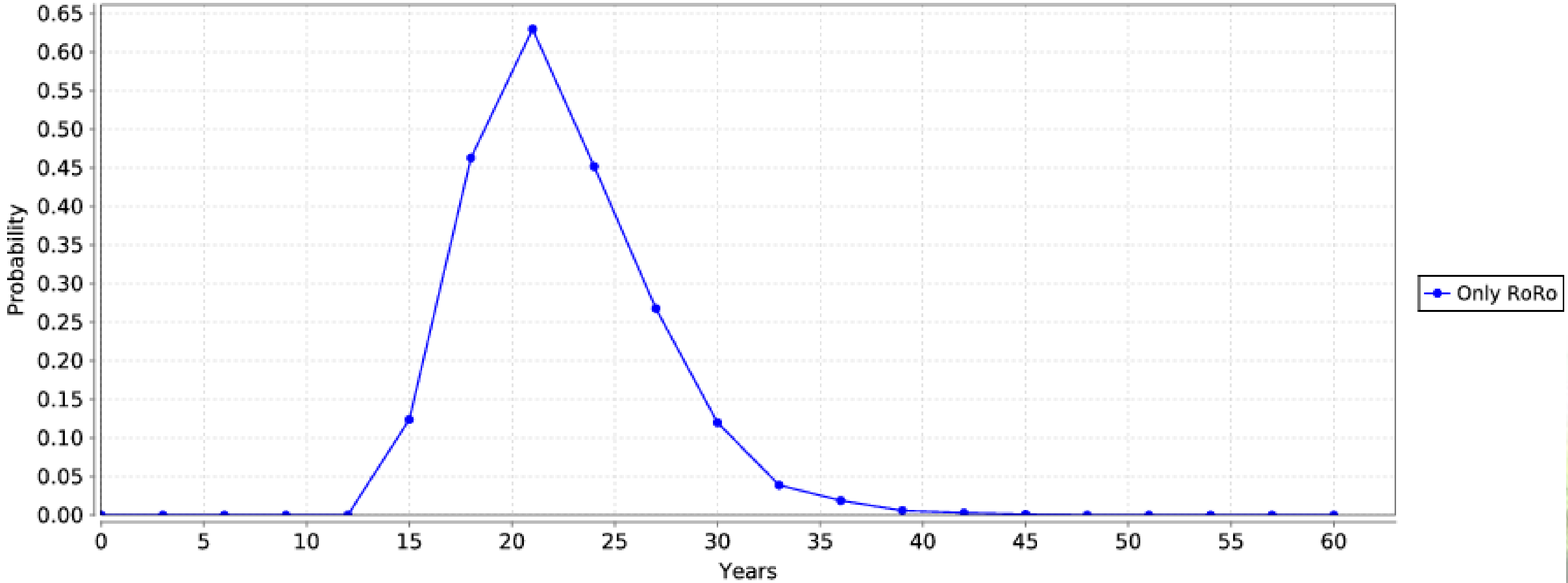


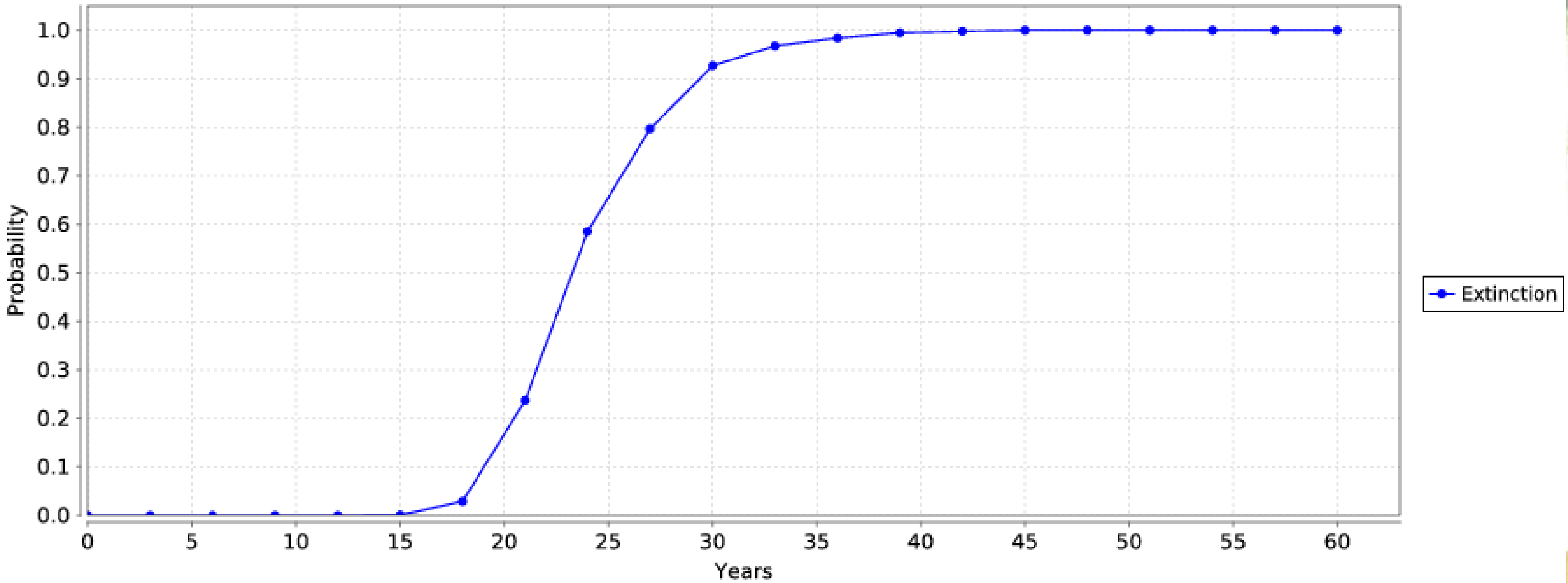
Dynamics of a L-E complex (simulation)

- all R genomes are mutation-free
- there is no sexual preference
- initial population: 95% of *P. lessonae* and 5% of *P. esculentus*



Statistical model checking: probabilities of P. ridibundus and Extinction





In this scenario **deleterious mutations are necessary** for the stability of L-E complexes

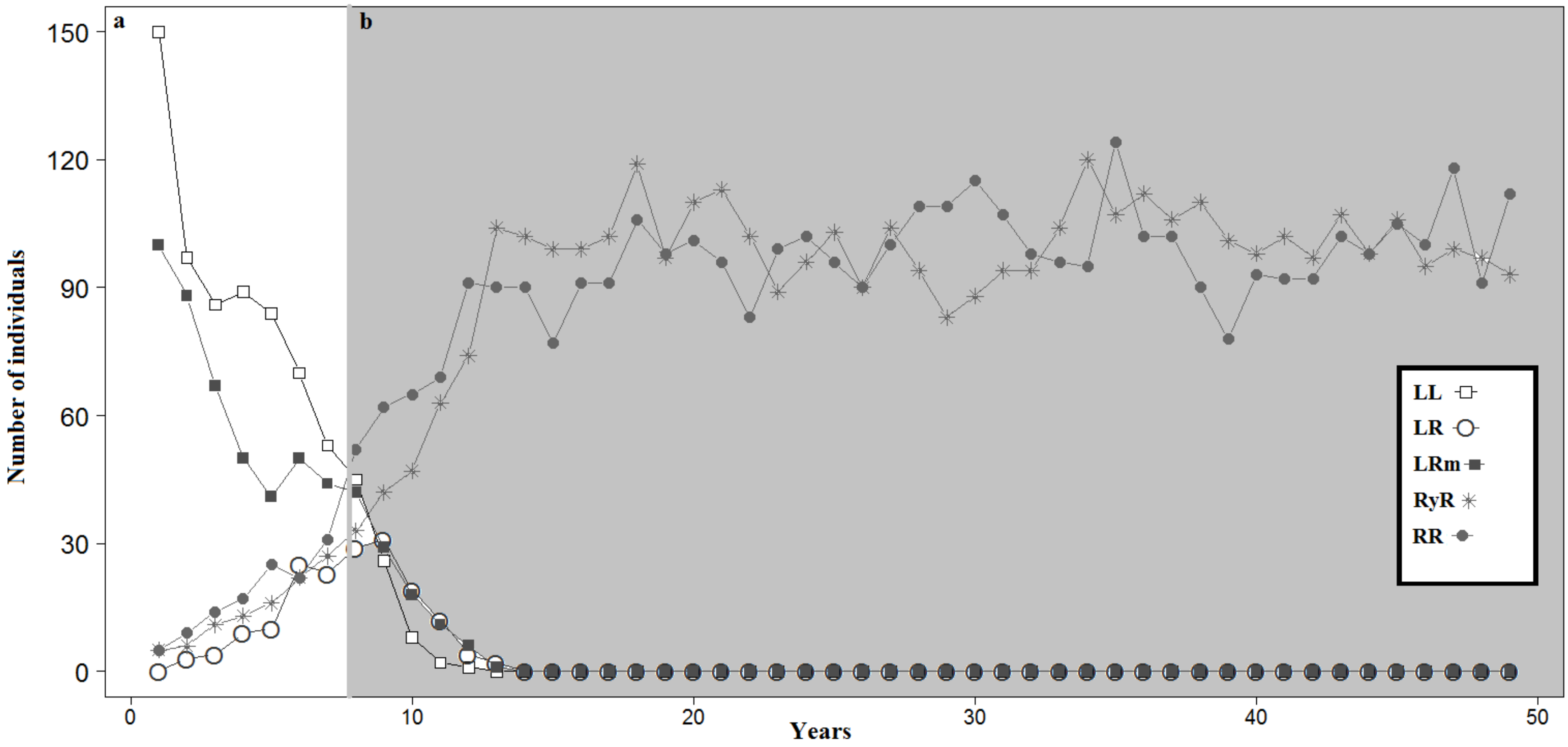
In all the existent Western Europe L-E complexes, generated *P. ridibundus* are inviable.

How L-E complexes react to the introduction of translocated *P. ridibundus*?

	LL 	LR 	RR 
L_yL 	L_yL LL	L_yR LR R_y	L_yR LR
L_yR 	LR	RR	RR
R_yR 	LR_y LR	RR R_yR	RR R_yR

How L-E complexes react to the introduction of translocated *P. ridibundus*?

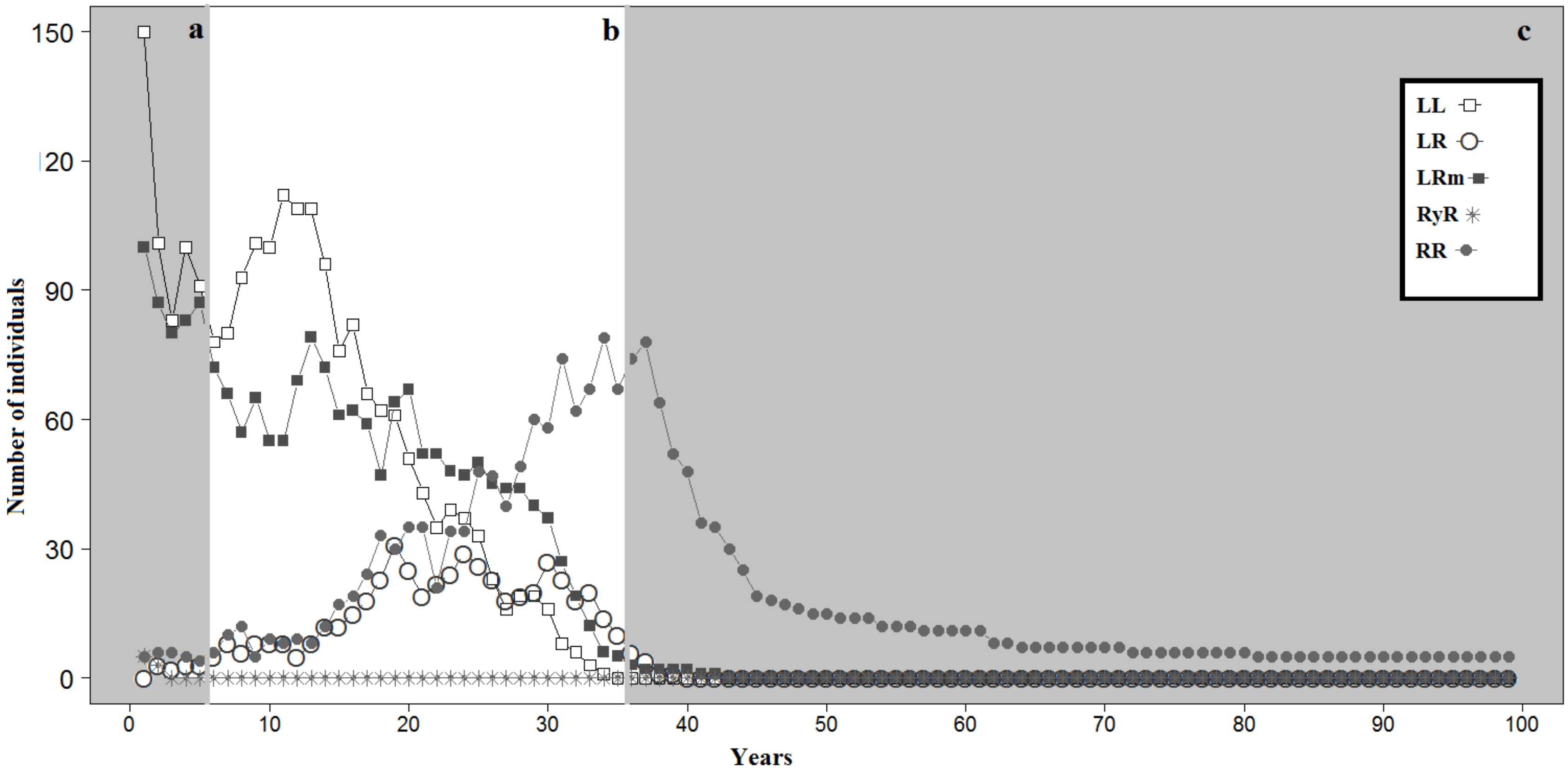
The result can be a monospecific *P. ridibundus* population…



How L-E complexes react to the introduction of translocated *P. ridibundus*?

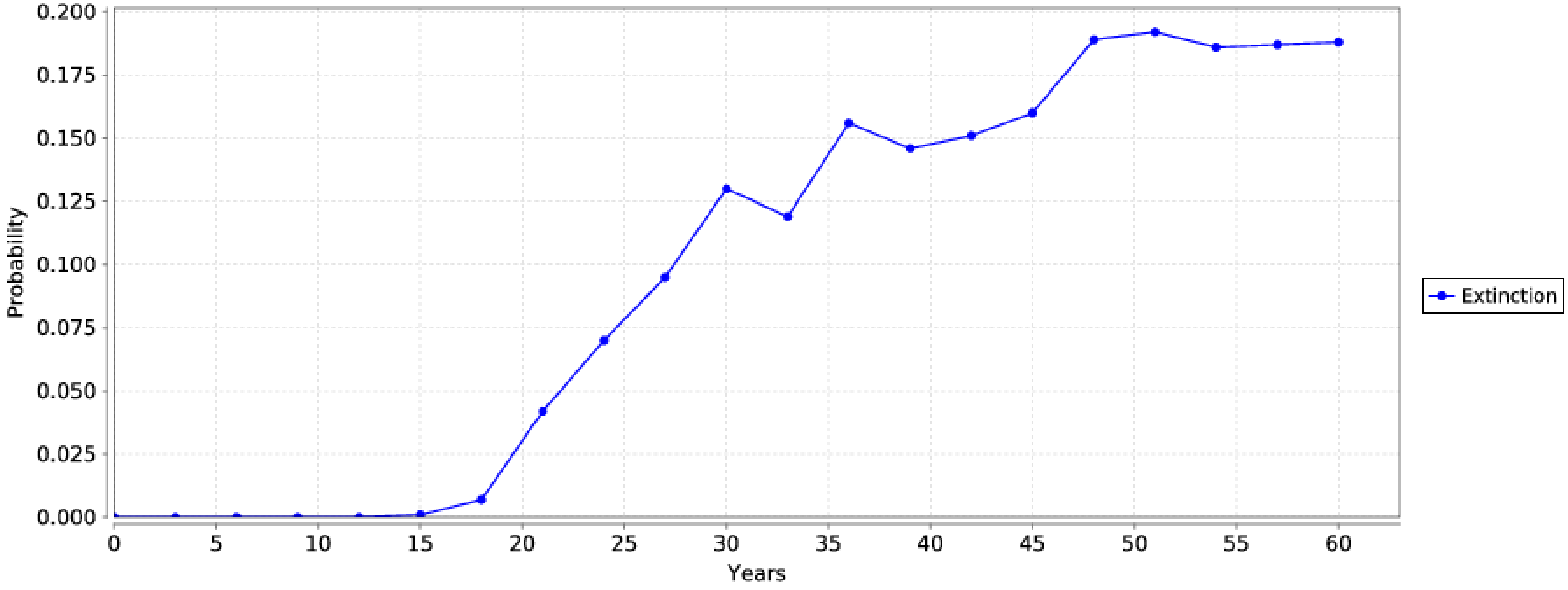
But *P. ridibundus* can suffer for an unsuitable environment so that they can be quickly eliminated, but they can introduce mutations free genomes in the L-E complex.

... and eventually the whole population collapses



Probability of extinction

- Statistical model checking (1000 simulations)



- Result: **0.18**

Conclusions

- P systems as an elegant notation for population models
- Simulation and statistical model checking as effective analysis techniques
- Case study on lake frogs: provided plausible answer to a currently open question in evolutionary biology

- **Further step:** Attributed Probabilistic P systems (APP systems) and their application to the modelling of social interactions in primates

References

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