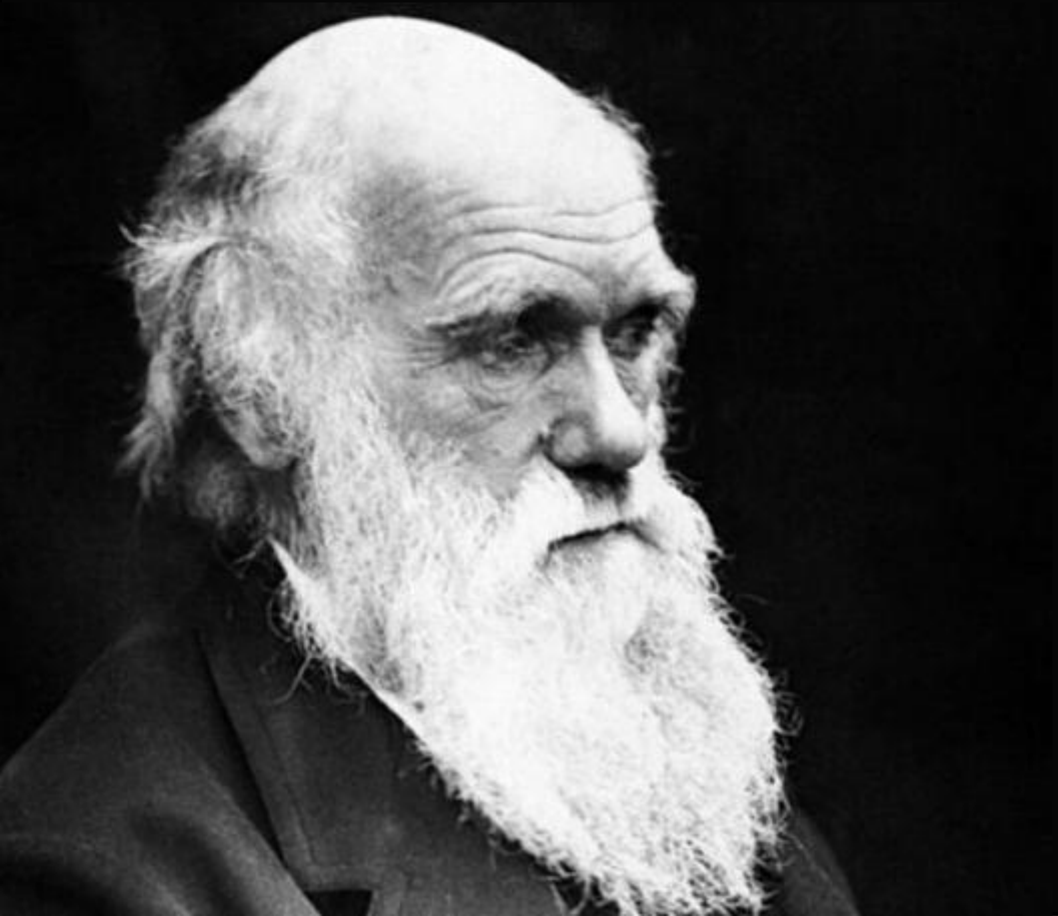
Eco-evolutionary dynamics

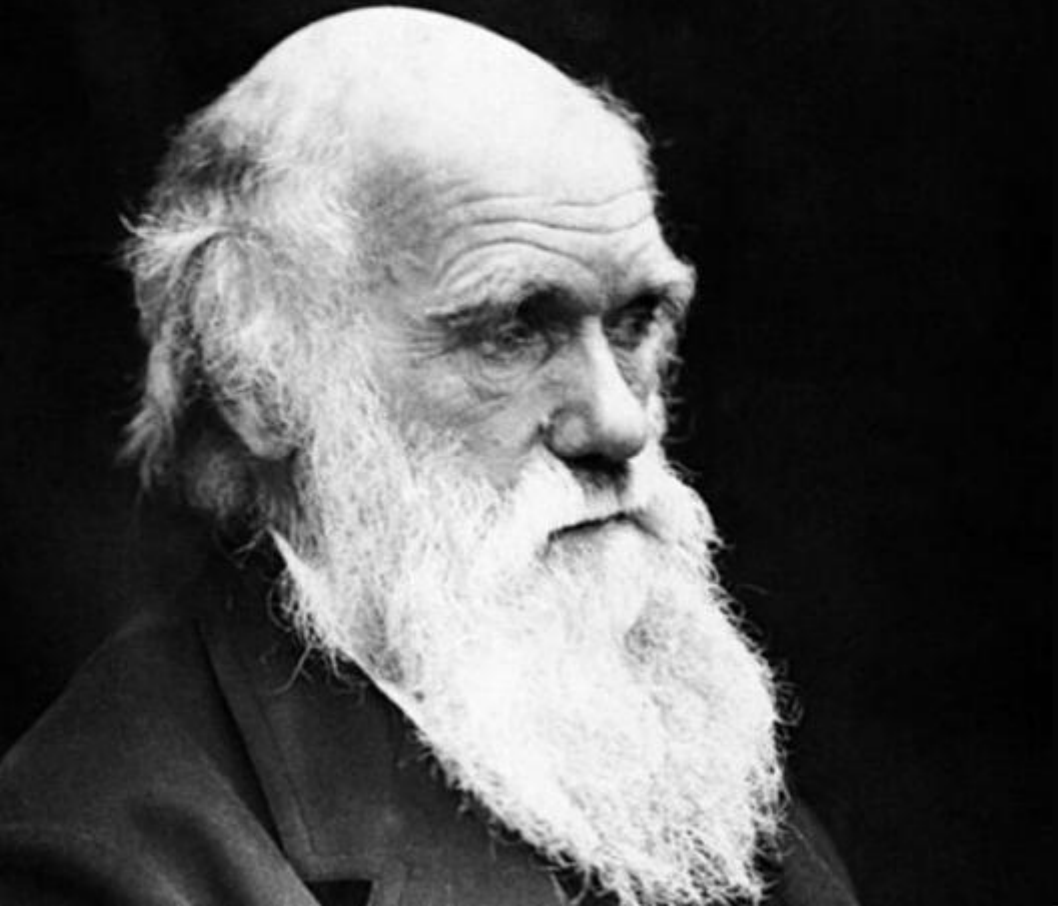
Interaction among species and the environment

Fabrizio Mafessoni, Biologia Evoluzionistica 2025/2026, Università di Trieste

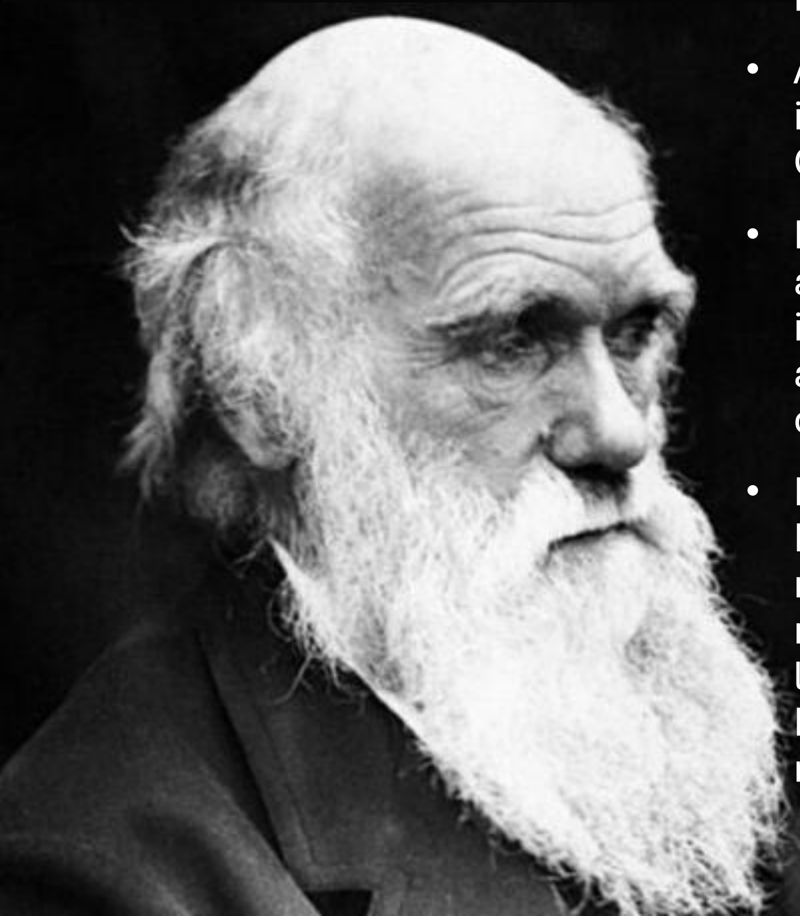


Today

- Examples of coevolution: mutualism, competition, commensalism
- How to model eco-evolutionary dynamics
- Niche construction and environmental feedbacks

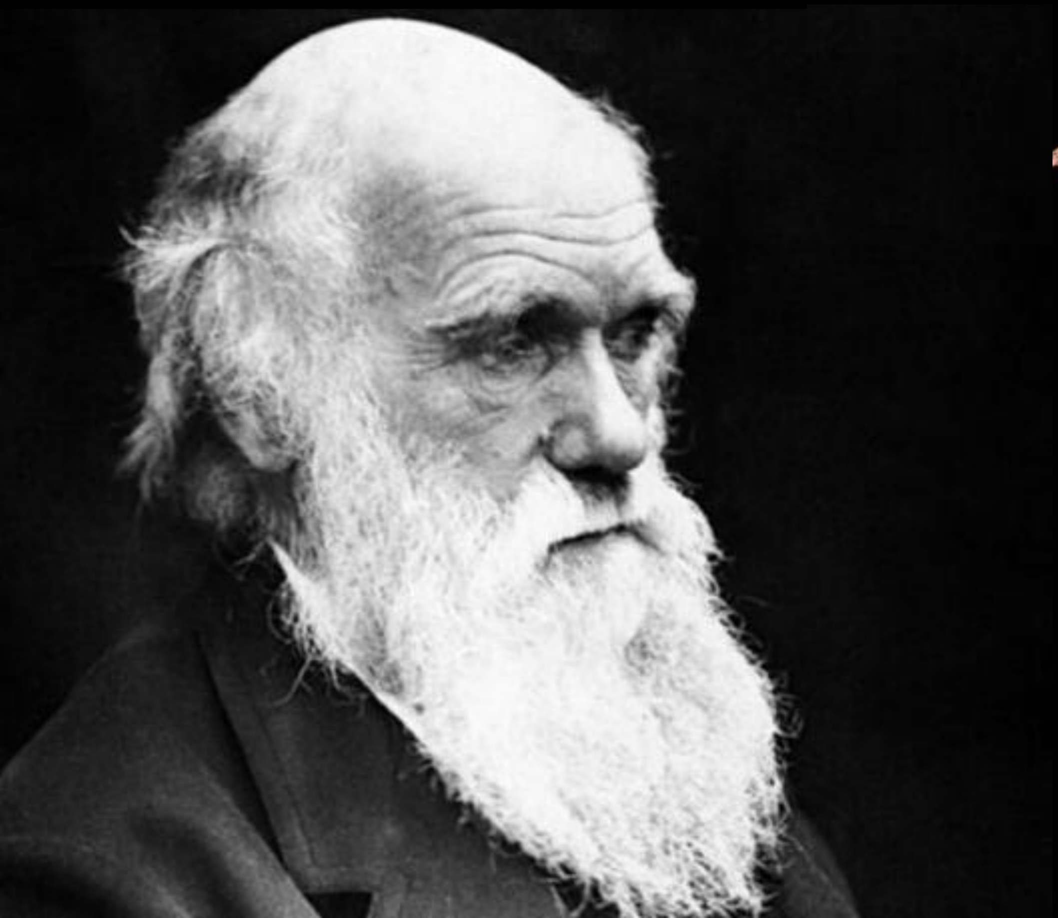


"On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing", Charles Darwin, 1862

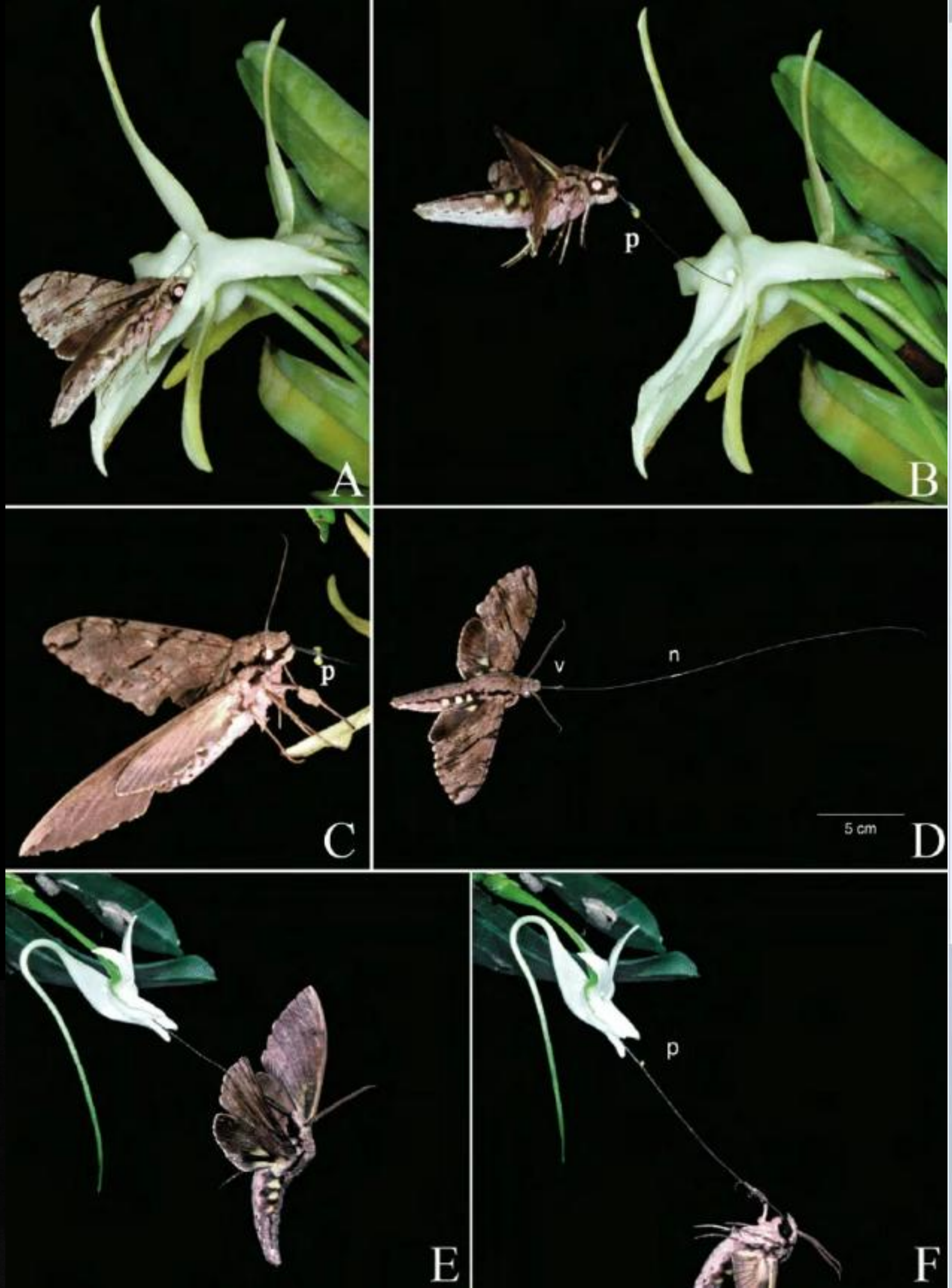


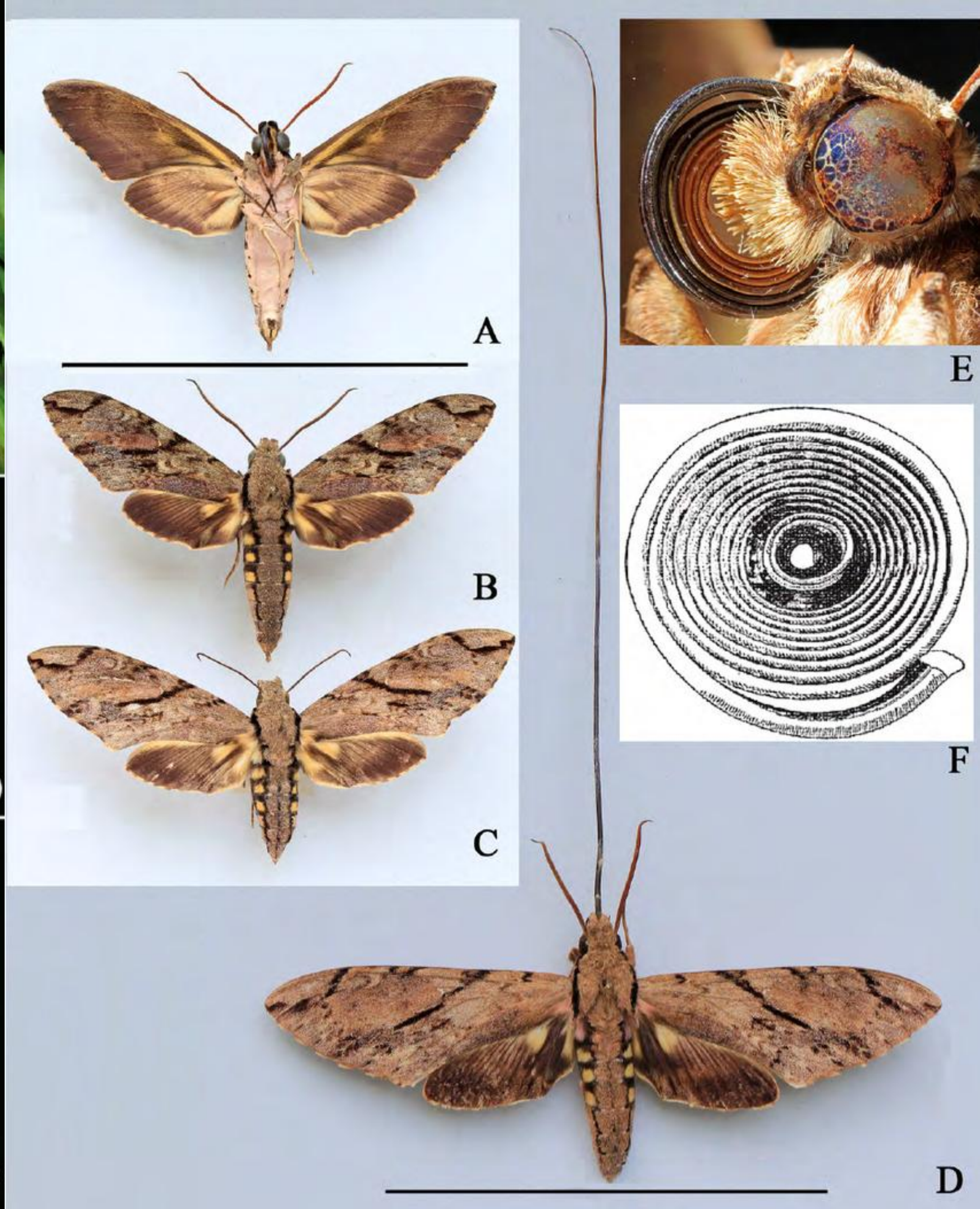
- In his first book after *On the Origin of Species* Darwin put into practice his principles of natural selection
- At the time, prevailing theological interpretation that flowers were shaped by God to inspire us with beauty
- Darwin showed that the astonishingly diverse and peculiar features of orchid flowers increase the chance that they attract insects and deposit pollen on them to ensure crosspollination
- He suggested that for a species from Madagascar, *Angraecum sesquipedale*, with a nectar-bearing tube up to 30 cm long, there must have existed a moth with a proboscis long enough. It wasn't known though, and Darwin was mocked for his ideas by a reviewer

in 1903 a sphinx moth with a proboscis up to 30 cm long was described from Madagascar, and was fittingly named *Xanthopan morganii praedicta*




I knew it!!!
Here is
Xanthopan morganii praedicta


A
B
p
C
p
v
n
5 cm
D
E
p
F


A
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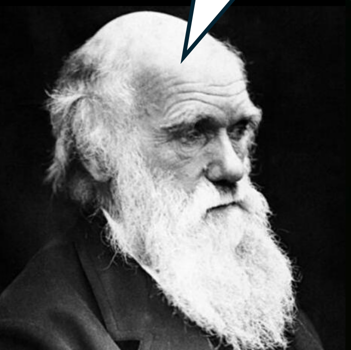
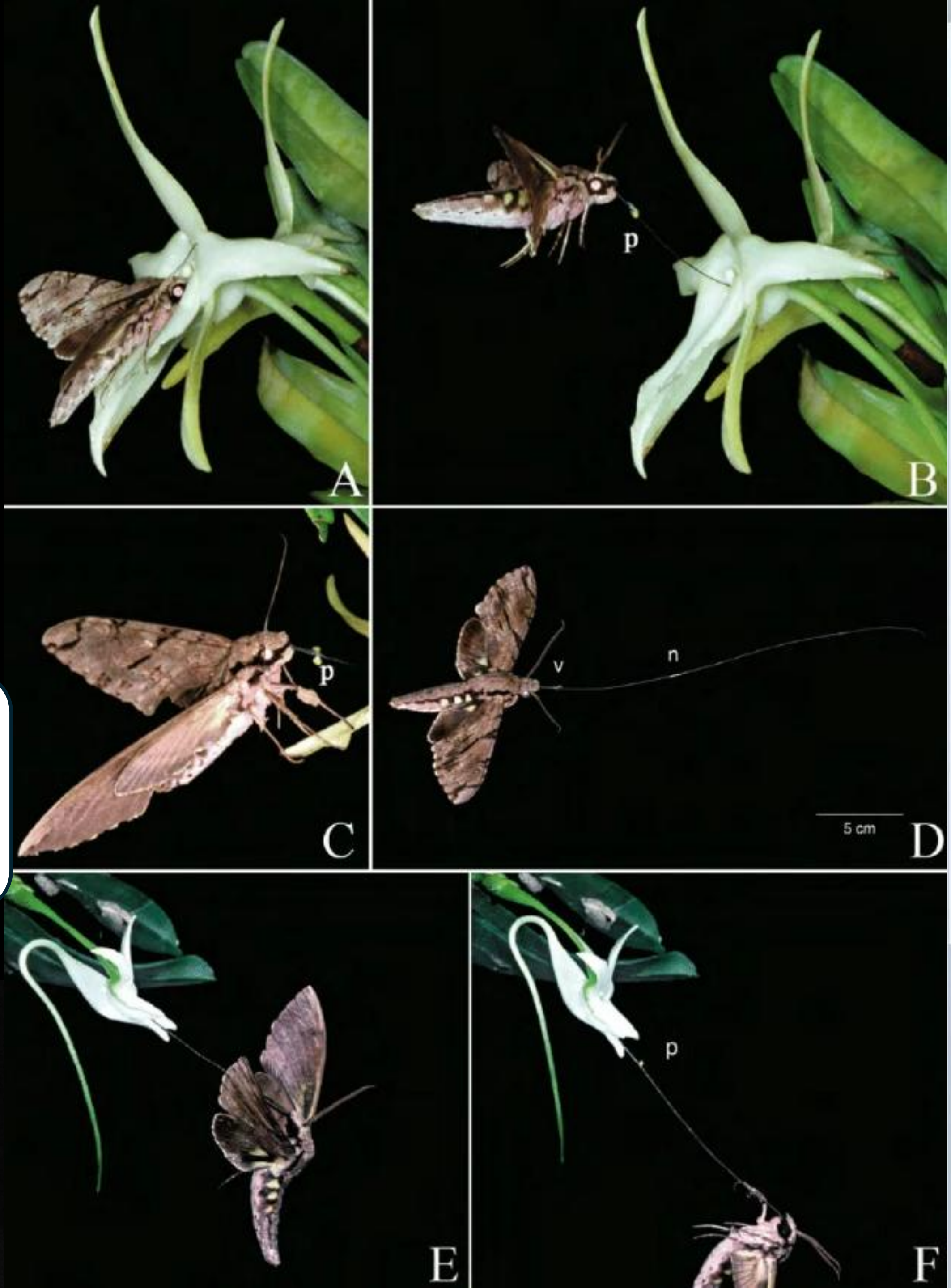
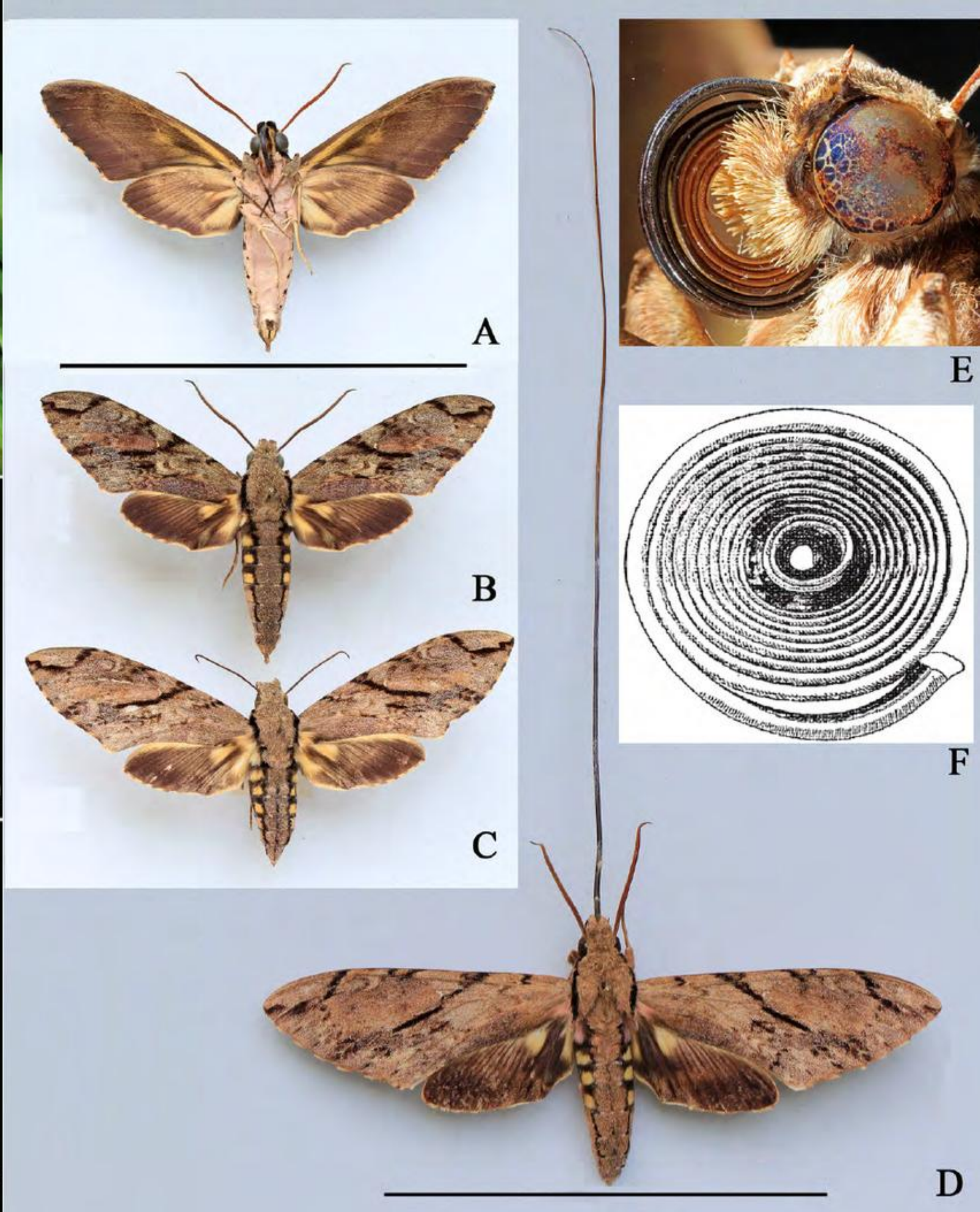
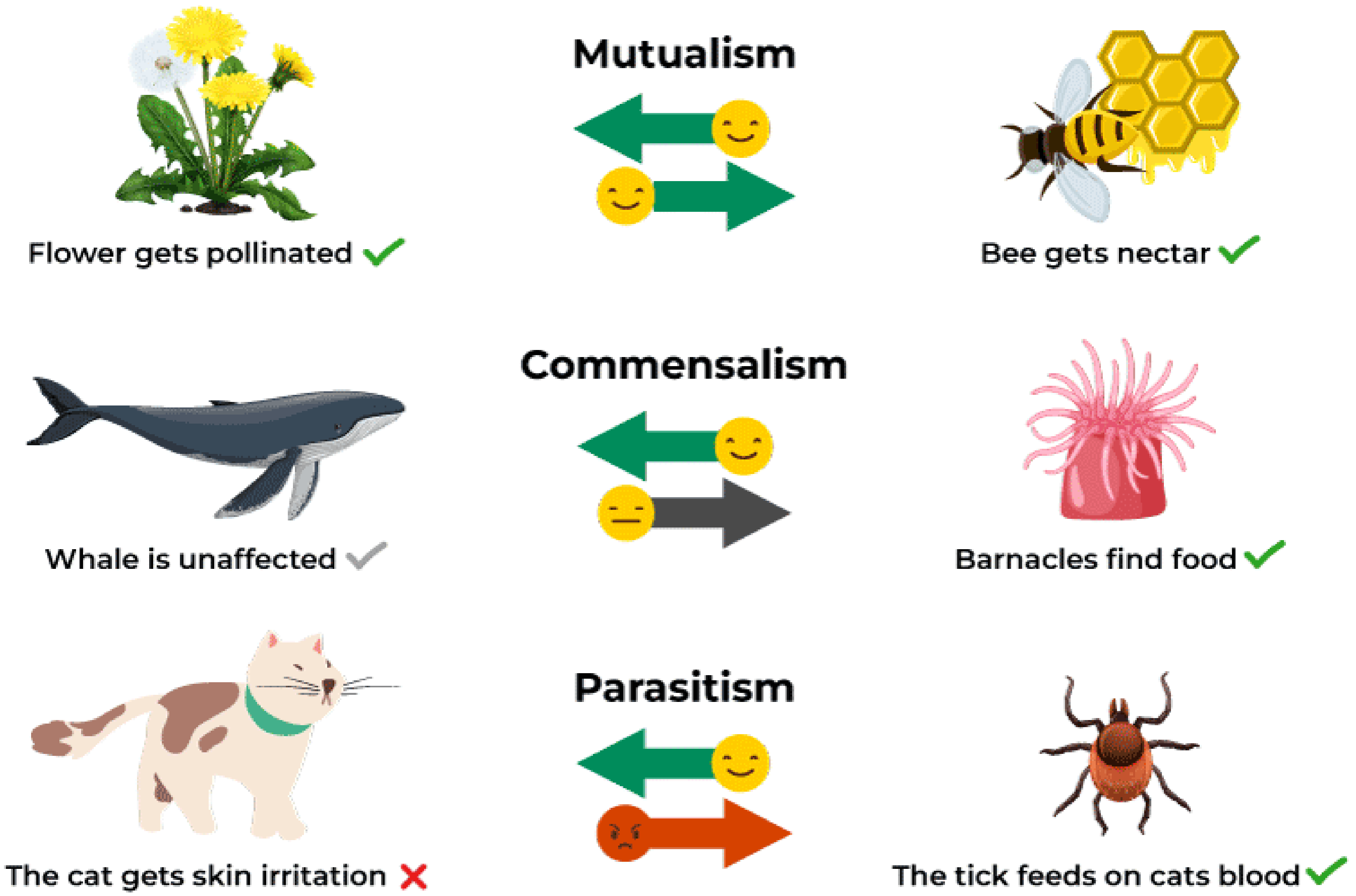
Evolution also implies **coevolution!**



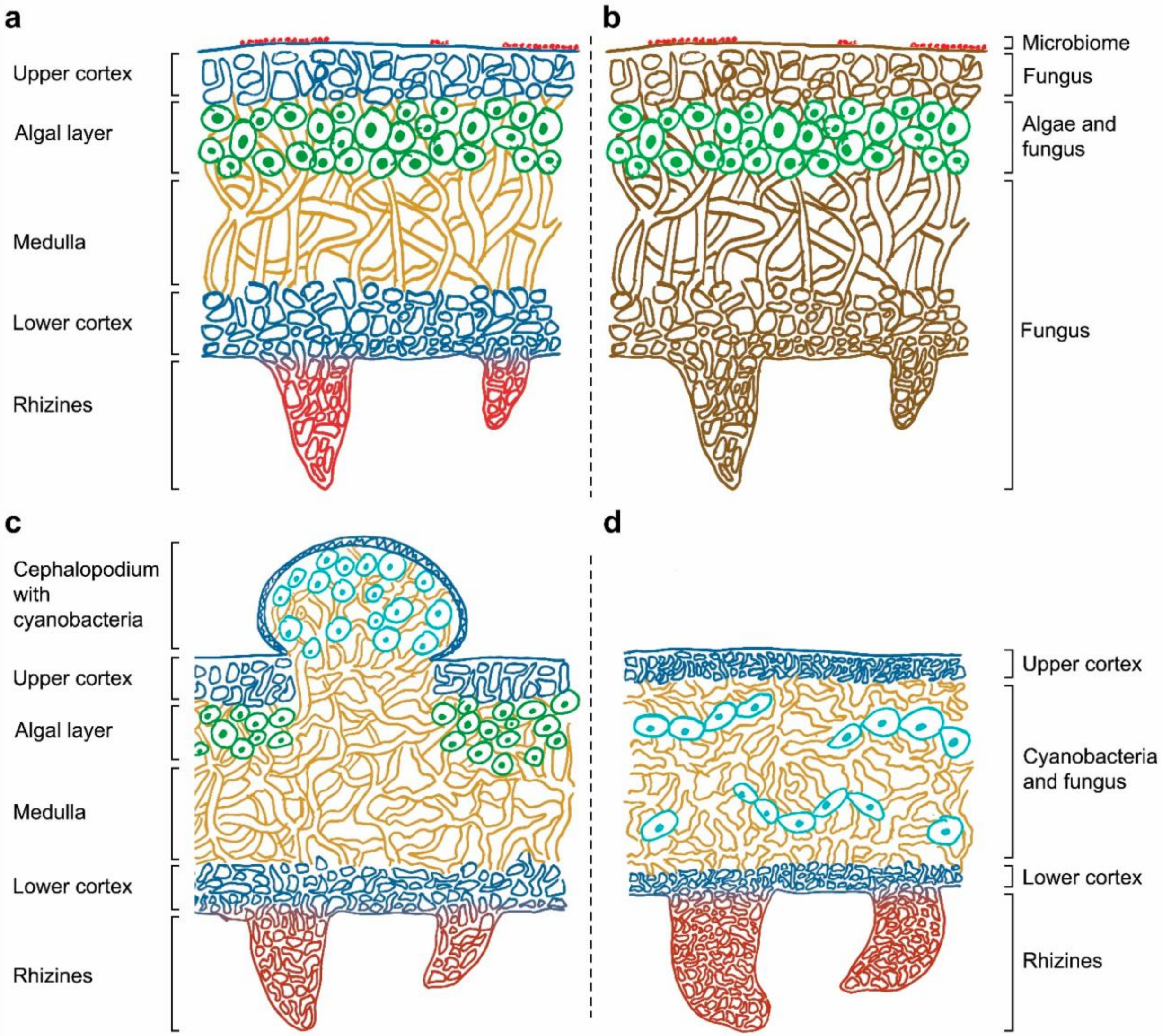





Mutualism
Flower gets pollinated
Bee gets nectar
Commensalism
Whale is unaffected
Barnacles find food
Parasitism
The cat gets skin irritation
The tick feeds on cats blood

Mutualism between fungi and algae: lichens

- Lichens are not a single organism but a **composite entity** — a stable symbiosis between a fungus (mycobiont) and a photosynthetic partner, either a green alga or a cyanobacterium (photobiont).
- **What each partner contributes:**
- **Fungus:**
  - provides physical structure and protection — it builds the thallus, retains water, shields the photobiont from UV radiation and desiccation, and secretes acids to extract minerals from rock
- **Photobiont:**
  - fixes carbon through photosynthesis, supplying sugars that feed both partners;
  - when the photobiont is a cyanobacterium, it may also fix atmospheric nitrogen



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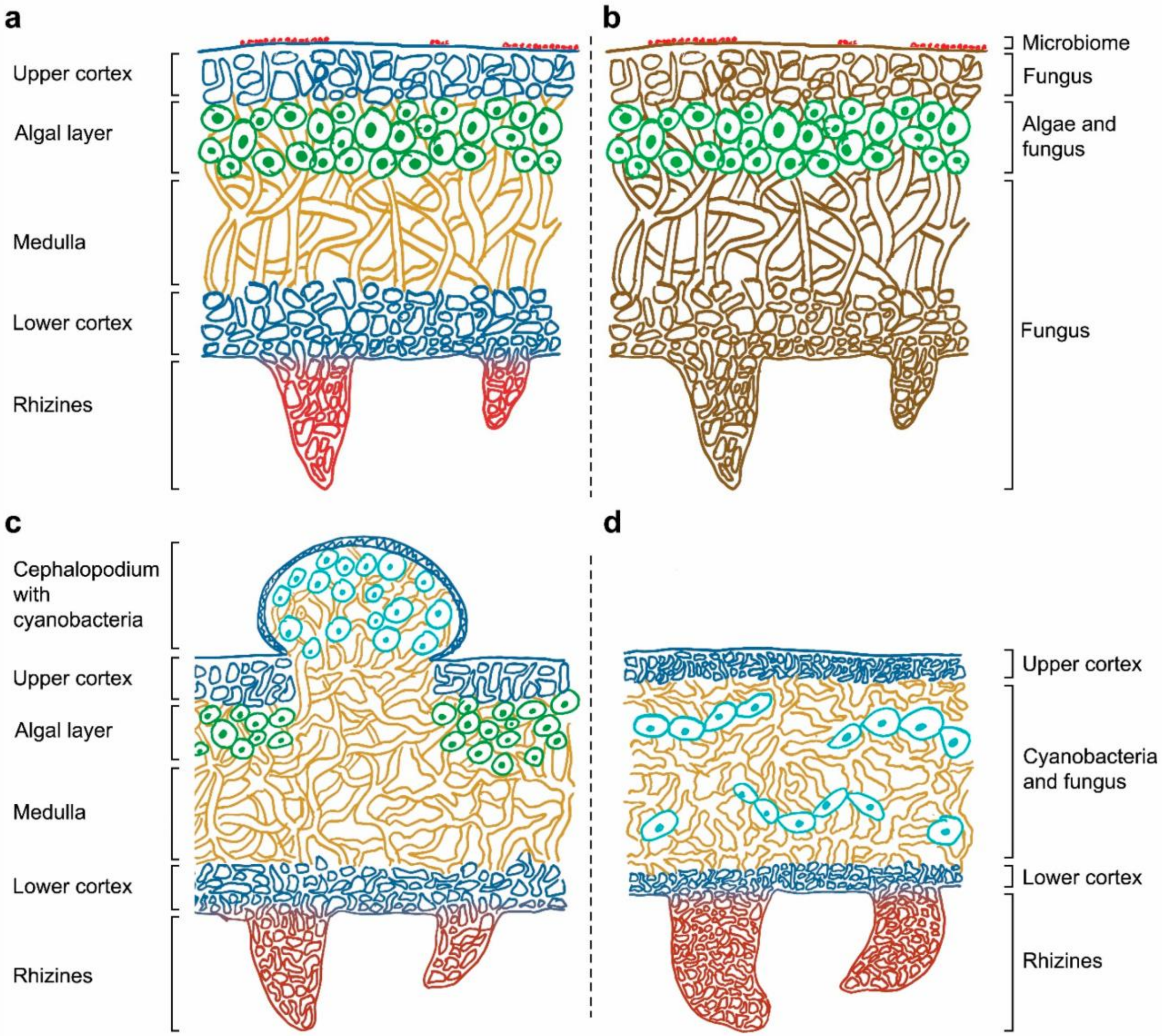
  - when the photobiont is a cyanobacterium, it may also fix atmospheric nitrogen
- **Why it is stable:** Neither partner can survive in the same habitats independently! Their fitnesses are **positively coupled** — each raises the other's survival in environments that neither could colonise alone, from bare rock to Arctic tundra.



Morillas et al.,2022, Encyclopedia

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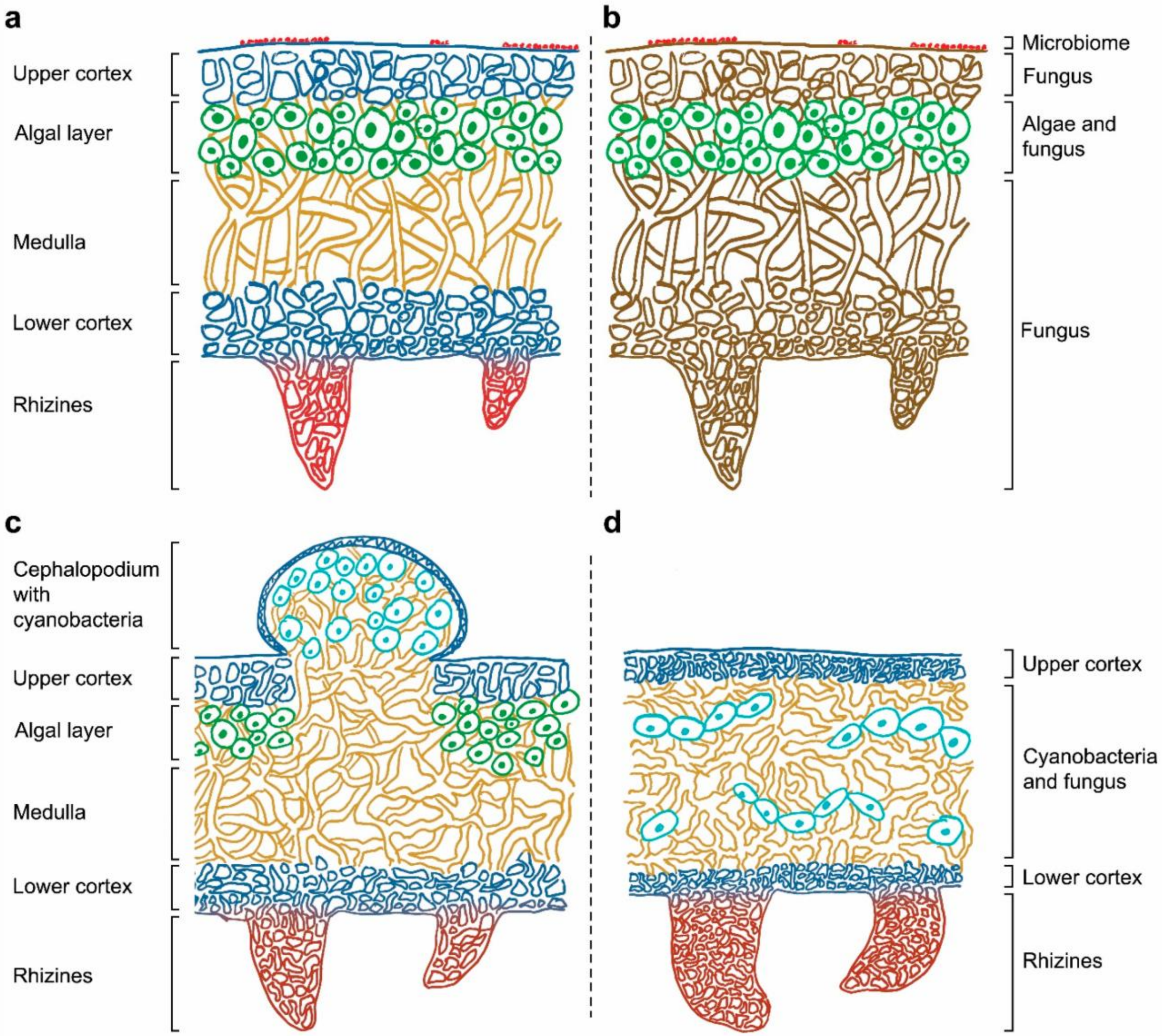
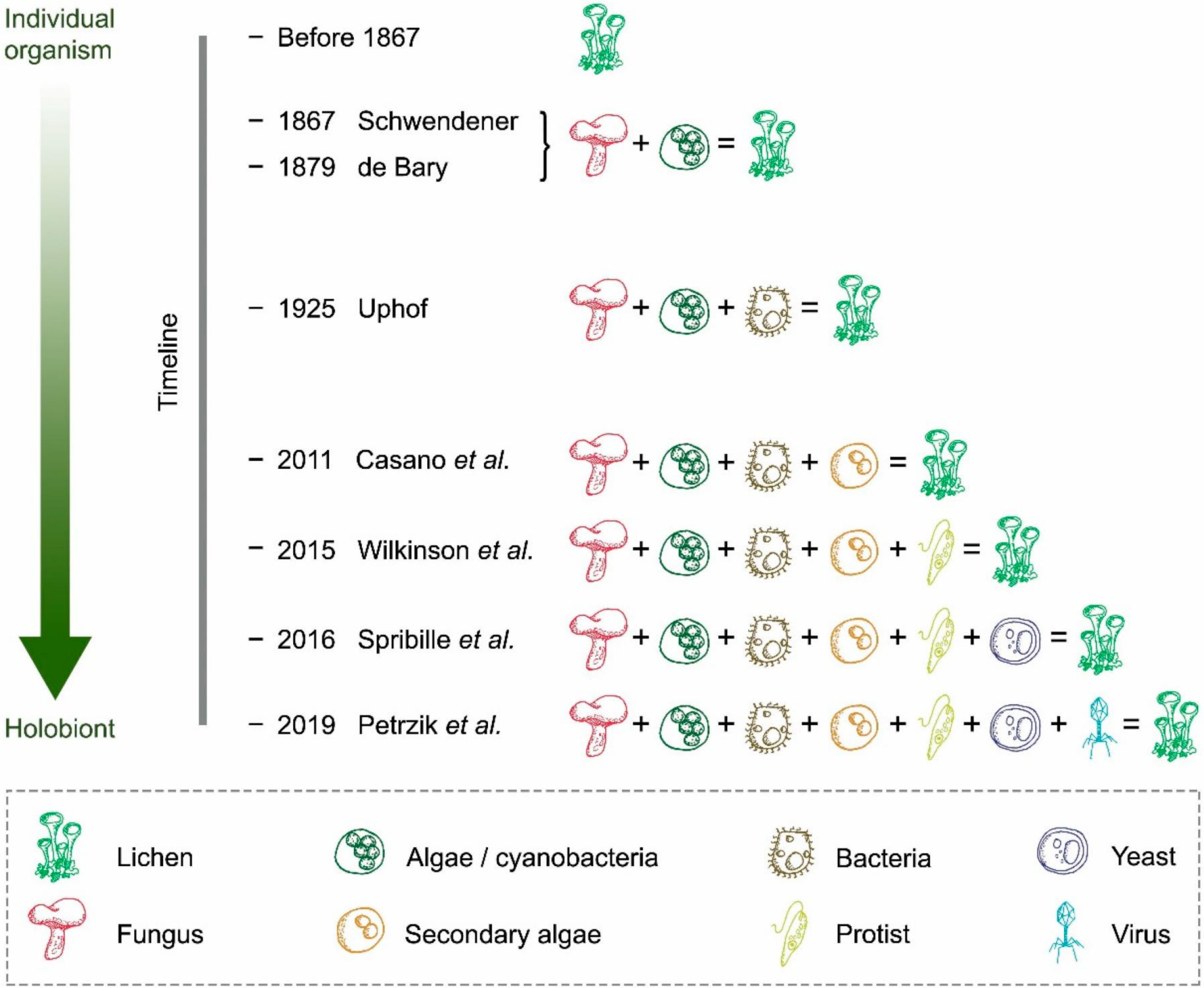


The evolutionary tension: The relationship is not perfectly harmonious. The fungus exerts some control — it can regulate photobiont cell division and extracts carbon at rates that may exceed what the photobiont would "give" freely. This places lichens on a continuum between **mutualism and controlled parasitism**.

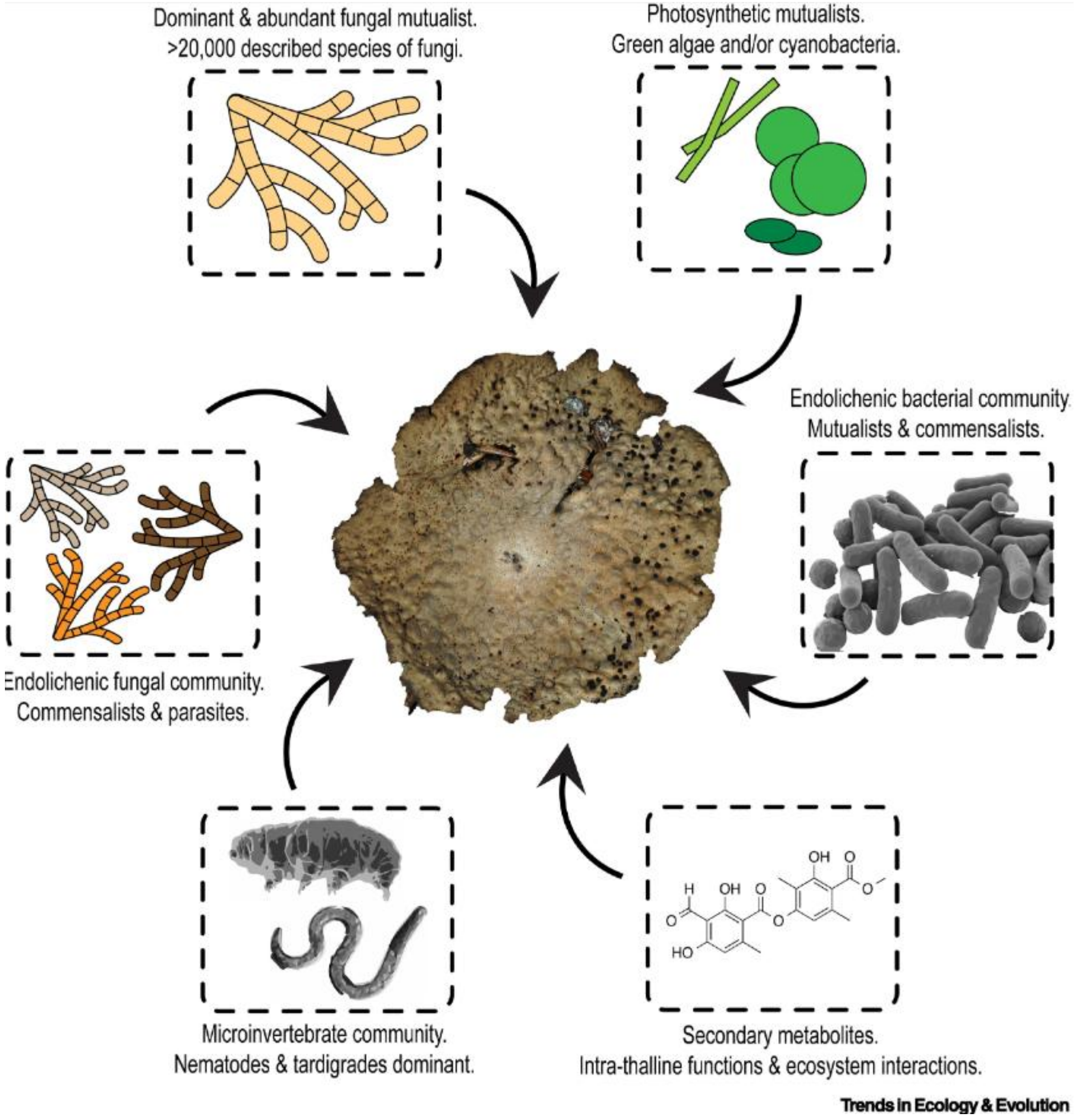
Lichens > fungus + algae!



Morillas et al.,2022, Encyclopedia

Lichens often represent more complex communities where commensalism and mutualism abound

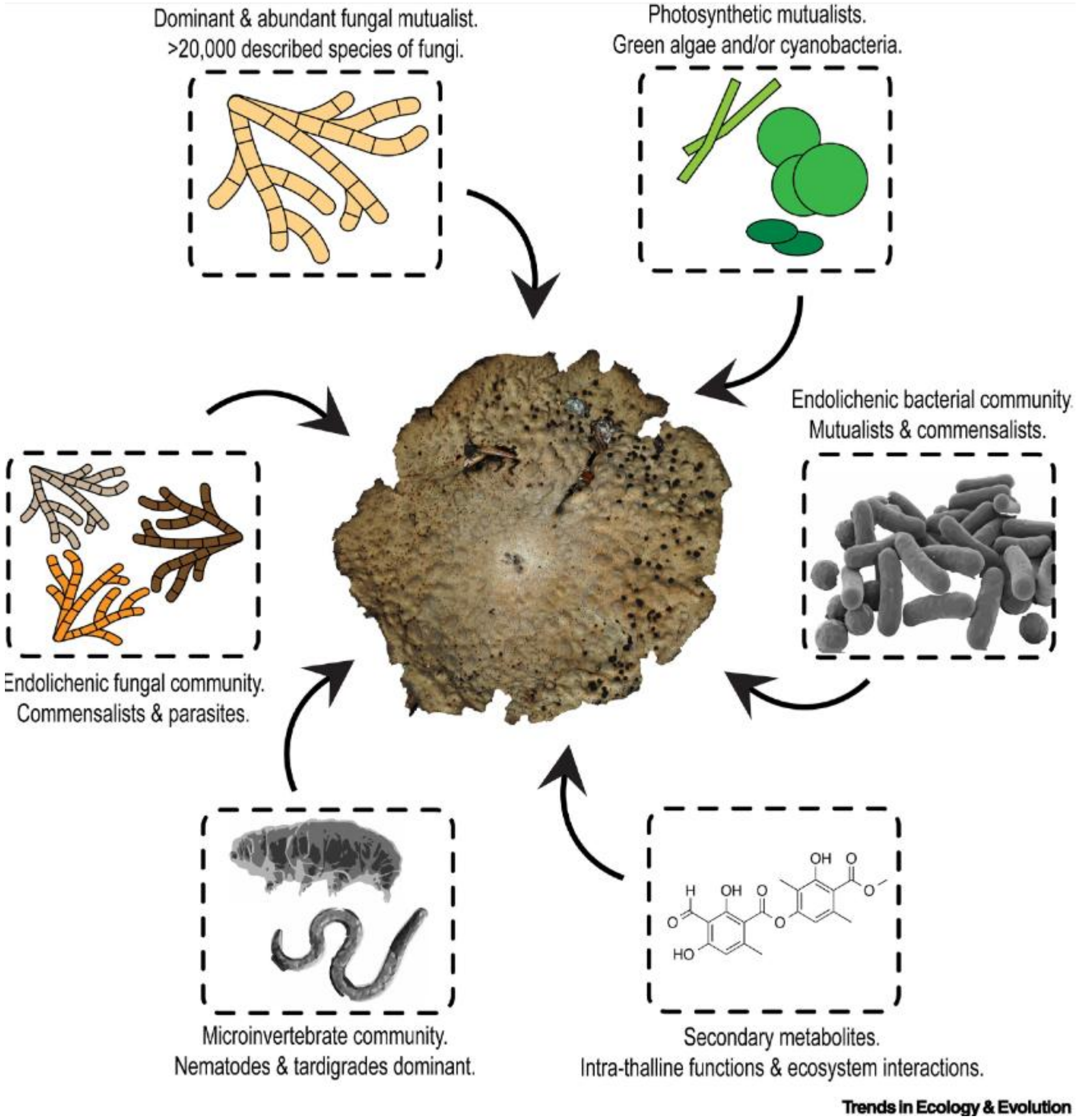
Allen & Lendemeier, 2022, TREE

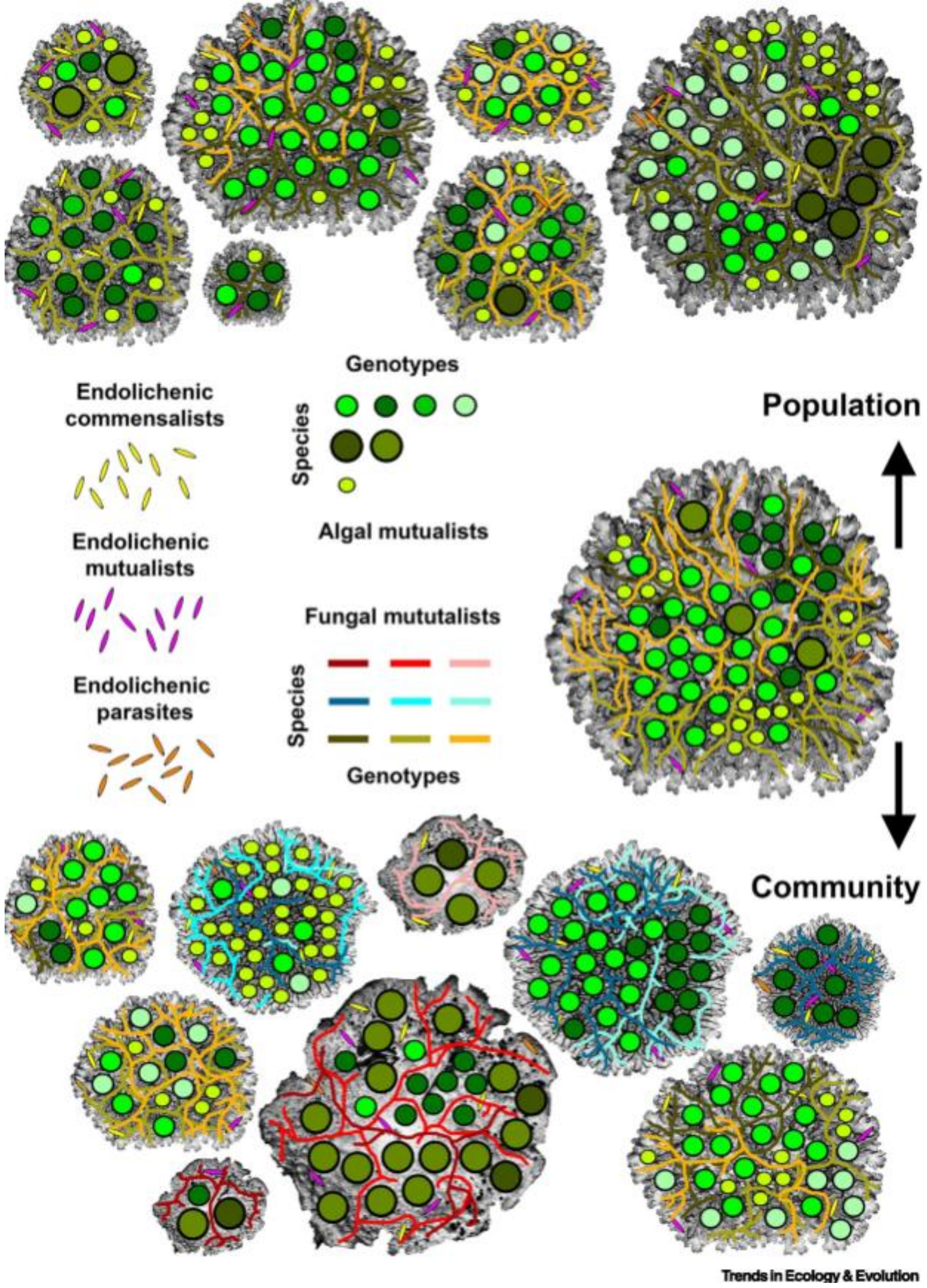


Lichens as a «holobiont»

Lichens often represent more complex communities where commensalism and mutualism abound

Allen & Lendemeier, 2022, TREE



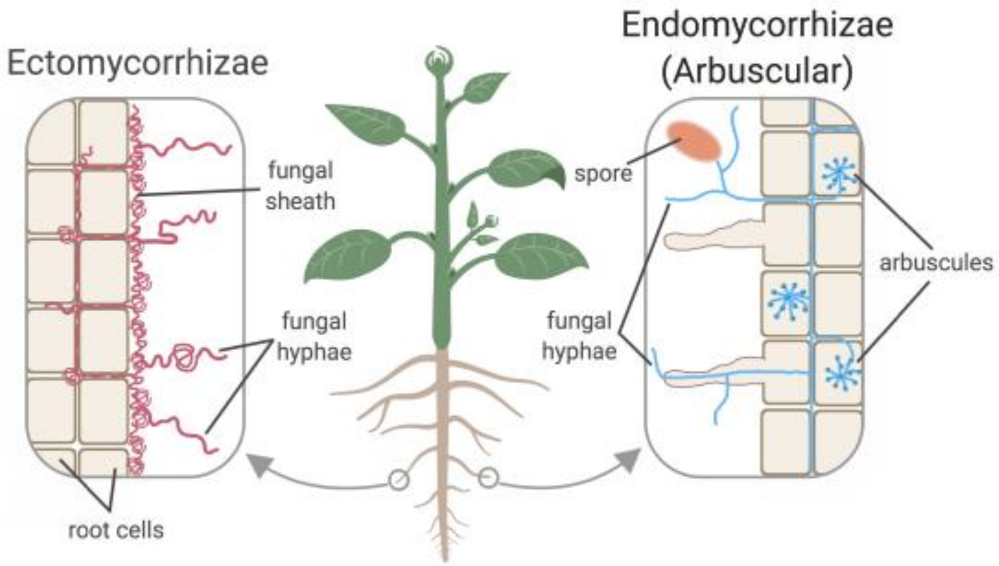


Mycorrhizae — Underground Trade Networks

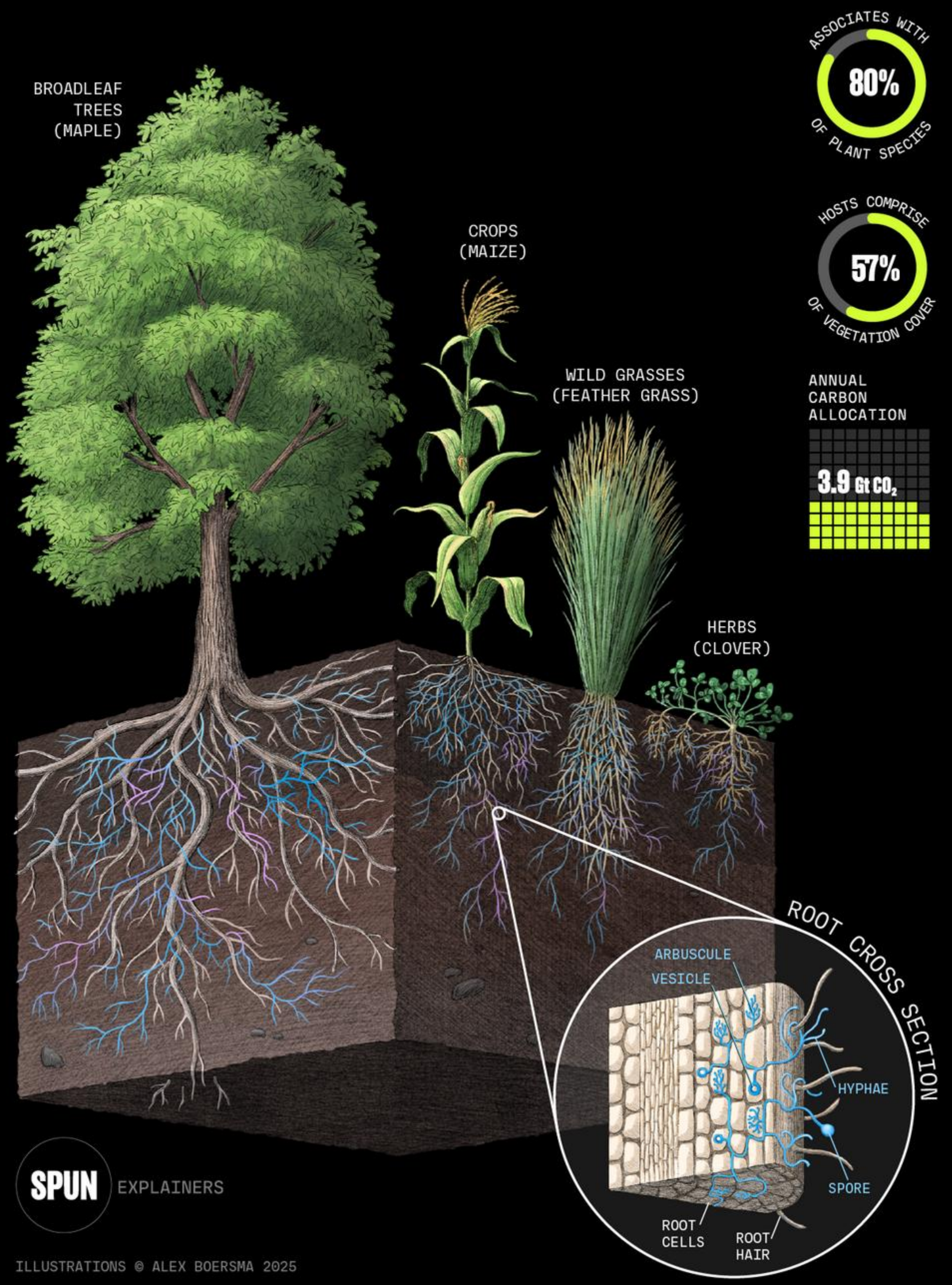
Mycorrhizae are symbioses between soil fungi and the roots of ~90% of all land plant species — arguably the most widespread mutualism on Earth, and the foundation of most terrestrial ecosystems.

What each partner contributes:

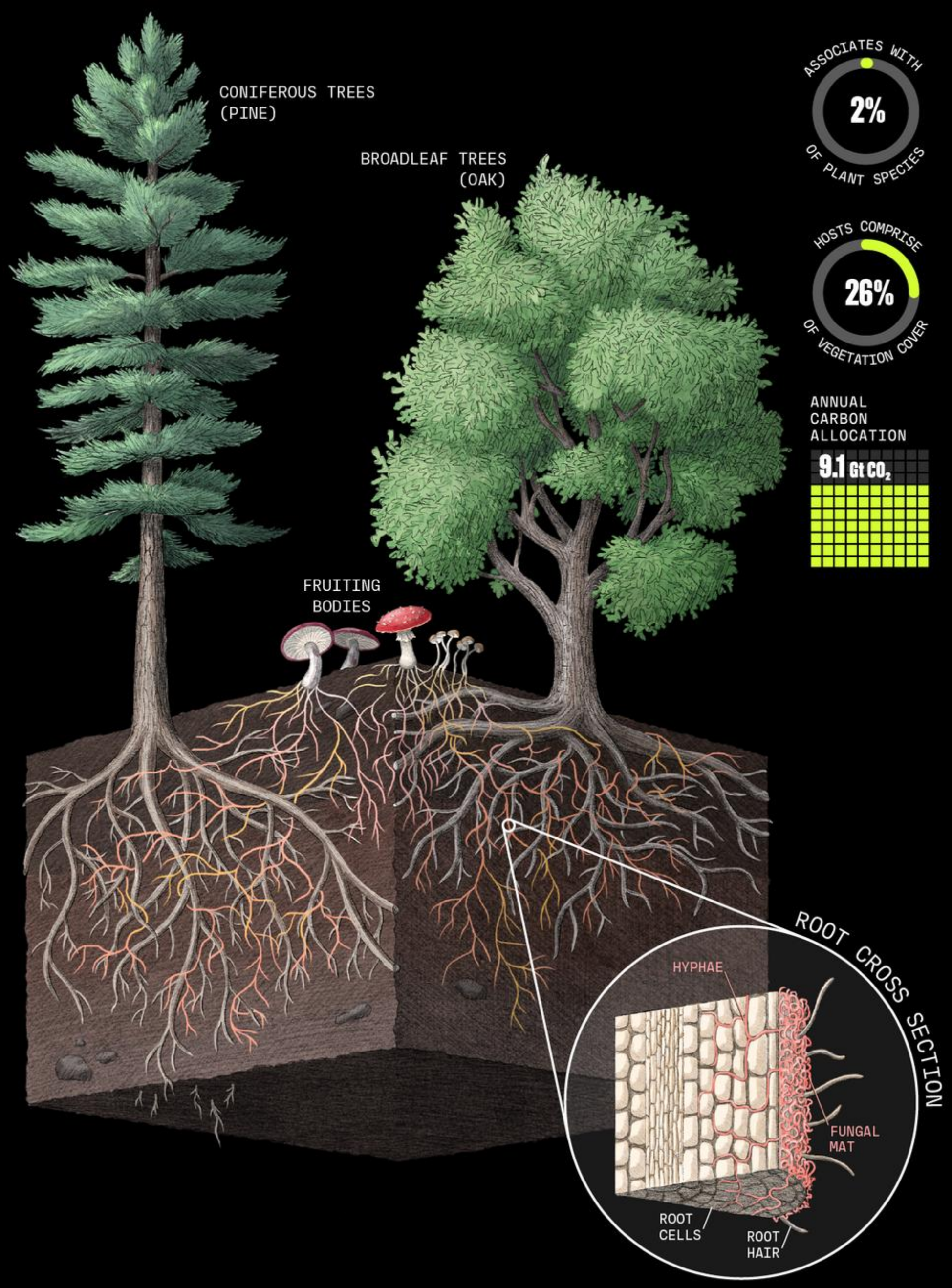
- The **fungus** extends the plant's effective root system by orders of magnitude through a vast network of hyphae, dramatically increasing uptake of phosphorus, nitrogen, and water from soil volumes the root alone could never reach
- The **plant** supplies the fungus with photosynthetically fixed carbon — sugars and lipids — which the fungus cannot produce itself, being entirely heterotrophic
- **Two main forms:**
- **Ectomycorrhizae** — hyphae wrap around root cells without penetrating them; typical of temperate forest trees (oaks, pines, beeches)
- **Arbuscular mycorrhizae** — hyphae penetrate root cells and form branched structures (arbuscules) for direct nutrient exchange; the ancestral and most widespread form, found in grasses, crops, and most herbaceous plants



Arbuscular Mycorrhizal (AM) Fungi



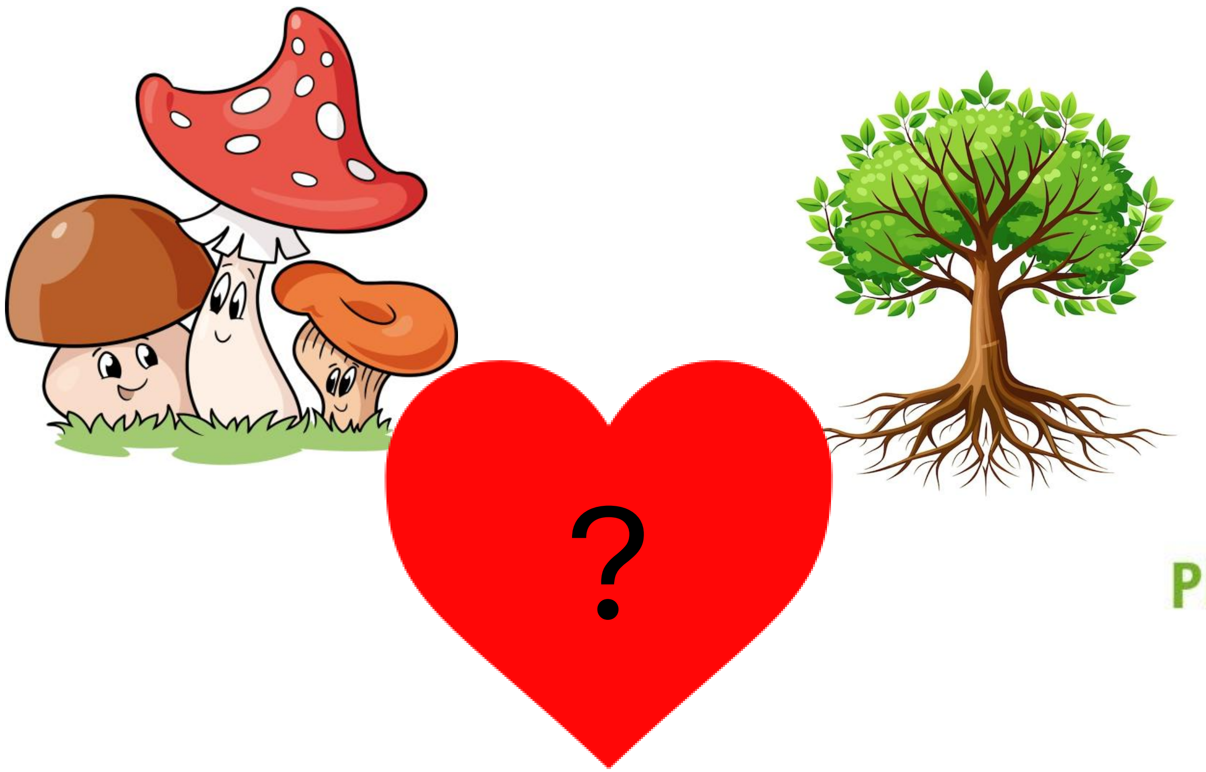
Ectomycorrhizal (EcM) Fungi

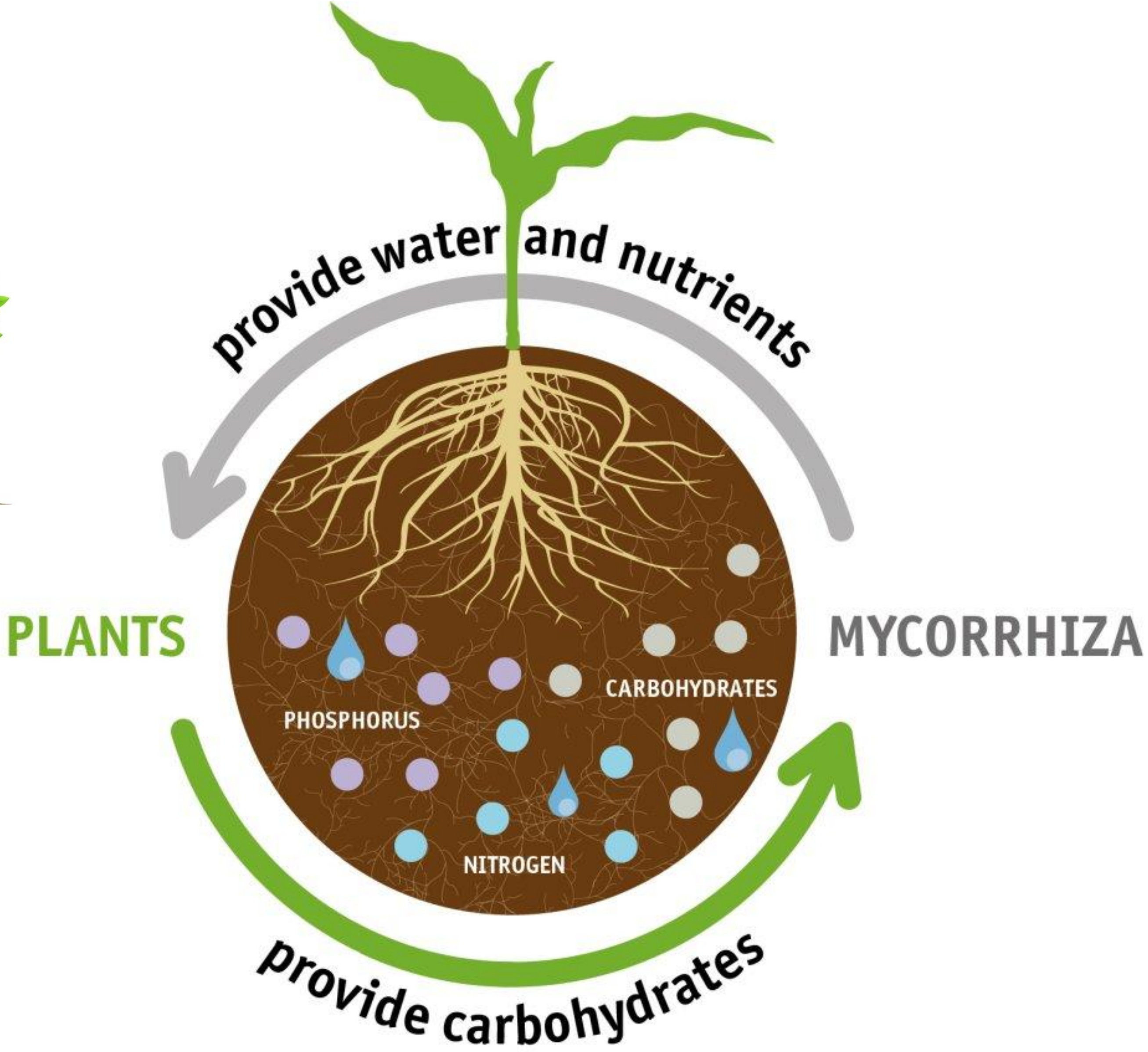


Mycorrhizae strongly benefit growth and the root system of plants


PSM Inoculated
Control

Do they always cooperate?





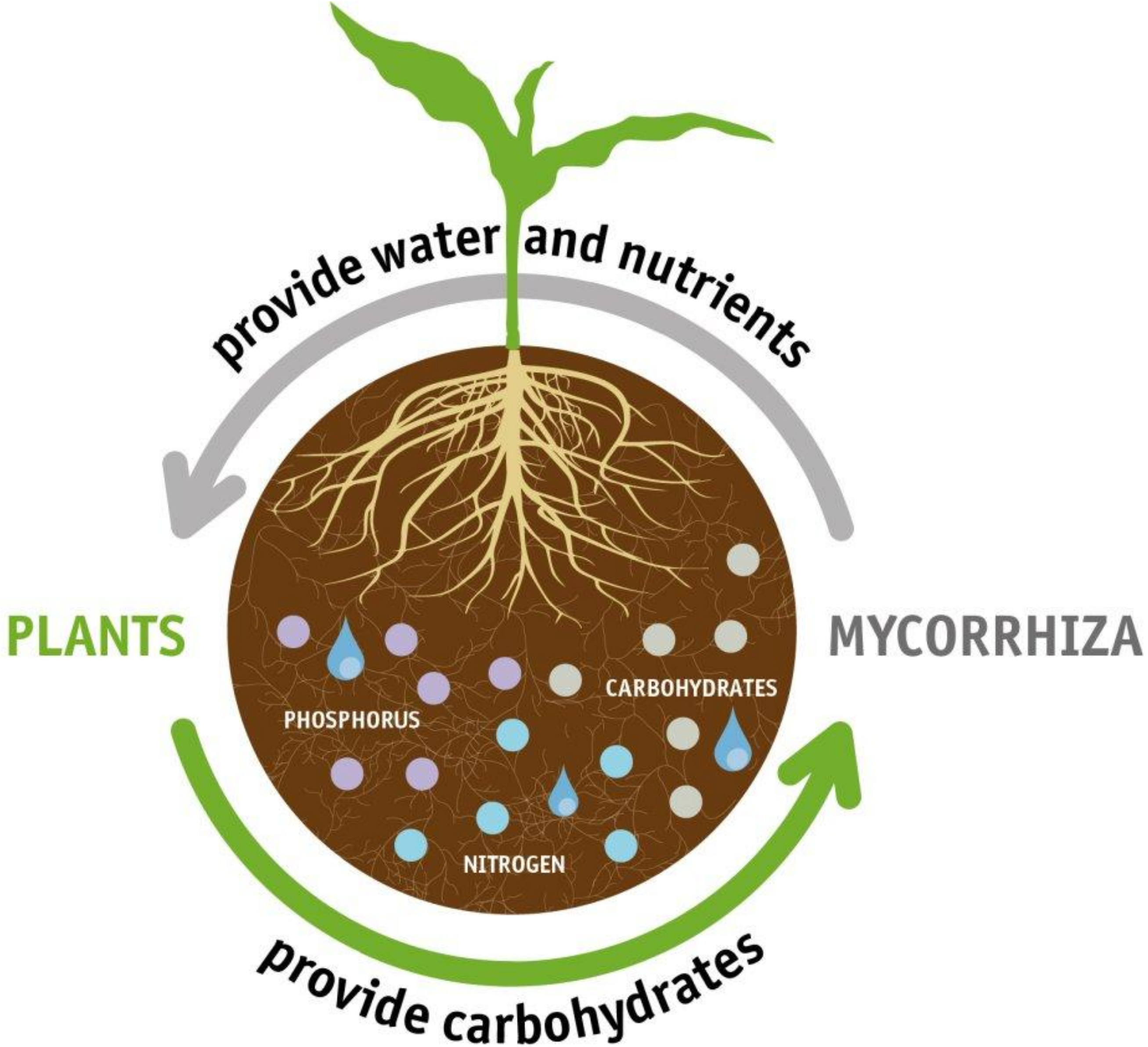
Do they always cooperate?

The evolutionary tension:

- As in lichens, the relationship sits on a continuum. Under high soil phosphorus, plants reduce carbon allocation to fungi — the mutualism weakens toward parasitism when the fungal service is less needed.
- Some fungal lineages have lost the ability to provide phosphorus and become **obligate cheaters**, exploiting the signalling system without contributing.

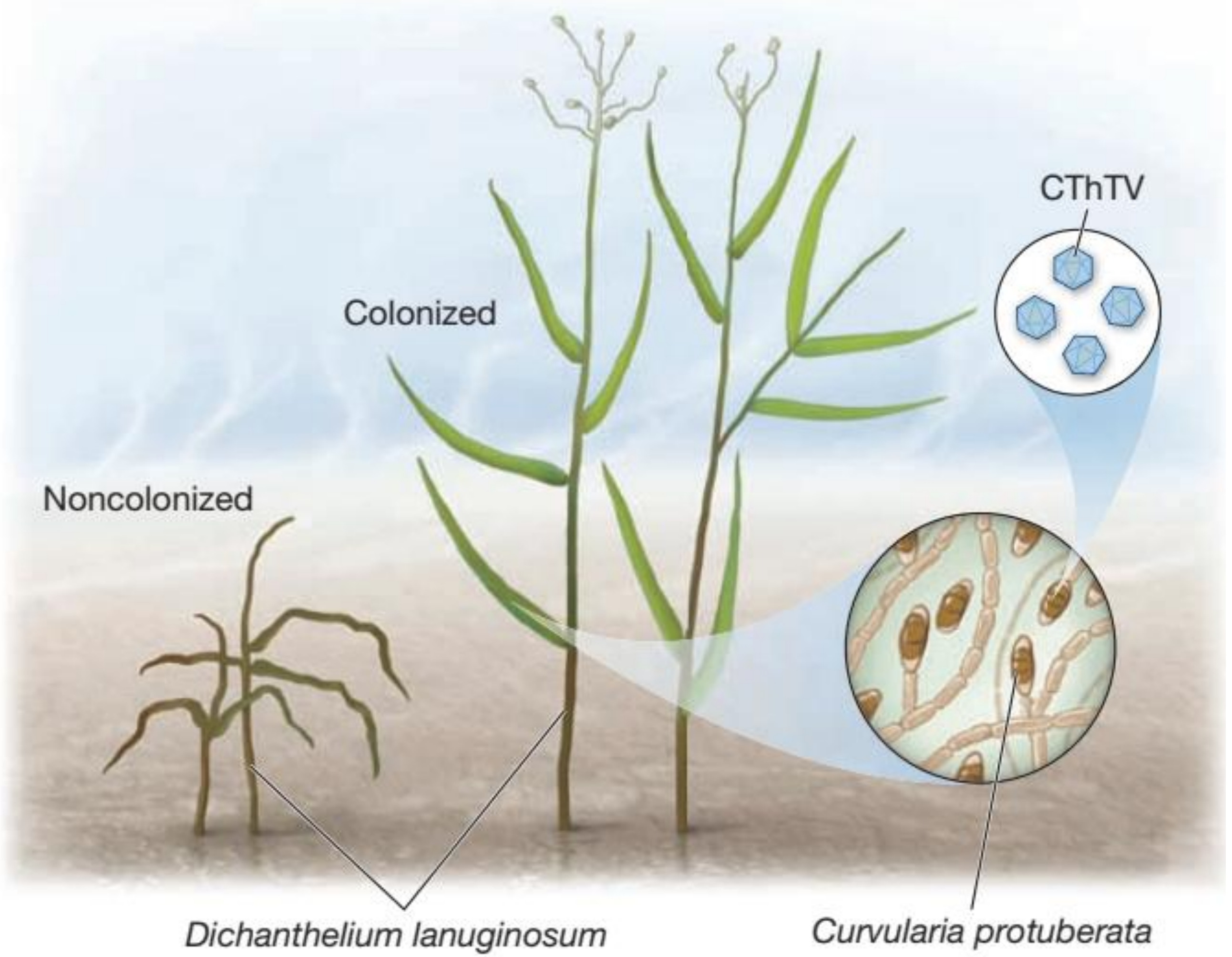
Why it is stable?

- The exchange is remarkably specific and regulated. Plants can **sanction** underperforming fungal partners by restricting carbon supply, and fungi can favour roots that offer more carbon.
- This creates a **biological market** — a decentralised trading system where cheaters are penalised and cooperative partners are rewarded, stabilising the mutualism without any central control.



Plant+fungus+virus

- The panic grass, *Dichanthelium lanuginosum*, can live in the geothermally heated soils of Yellowstone National Park, where soil temperature often exceeds 130°F.
- To survive, the plant requires the presence of a fungus, *Curvularia protuberata*.
- For the fungus to survive in the soil, it in turn requires that a virus, called the *Curvularia* thermal tolerance virus (CThTV), be present in the environment (Marquez et al. 2007).
- Mechanism still unclear, but the presence of the virus affects the expression of Heat Shock Proteins and some osmoprotectant.
- Probably a case of non-specialized "**diffuse mutualism**".




Is it all ?

Is it all love?

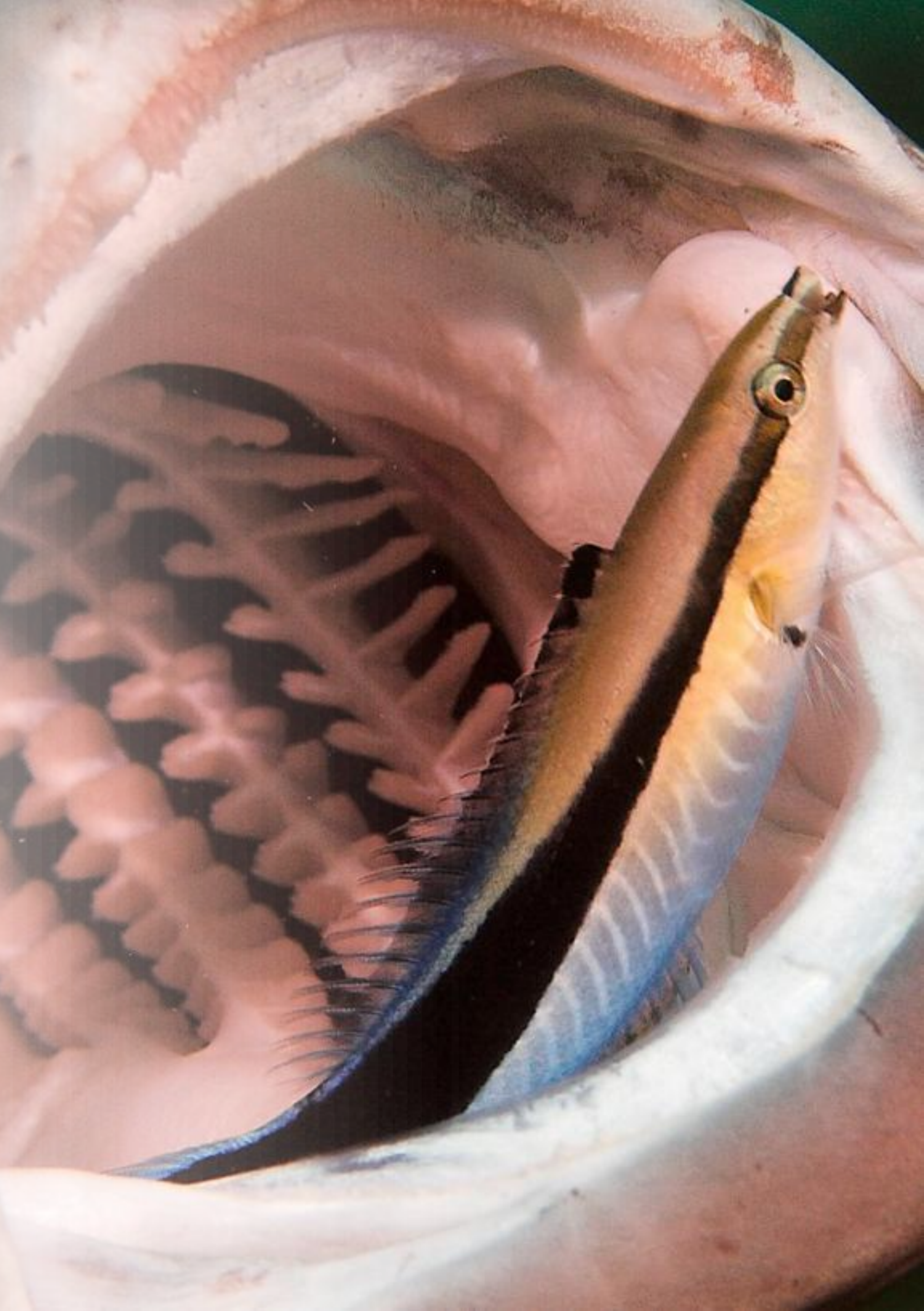
The Basic Mutualism: Cleaner fish (like cleaner wrasses) remove parasites, dead tissue, and mucus from **client fish**. Clients benefit from parasite removal and wound cleaning; cleaners get a nutritious meal. Both parties benefit — classic mutualism.

Where the Tension Arises

- The evolutionary conflict centers on **what the cleaner chooses to eat:**
  - **Cooperative strategy**: eat parasites and dead tissue — benefits the client, sustainable food source for cleaner
  - **Cheating strategy**: bite healthy tissue, scales, or mucus — immediate nutritional gain for cleaner, but harms the client
- **The client's dilemma**: it's vulnerable while being cleaned (stationary, mouth and gills open), so it risks exploitation. But it needs the cleaning service.
- **The cleaner's dilemma**: healthy tissue is often more nutritious than parasites, but biting clients drives them away and destroys the long-term food source.

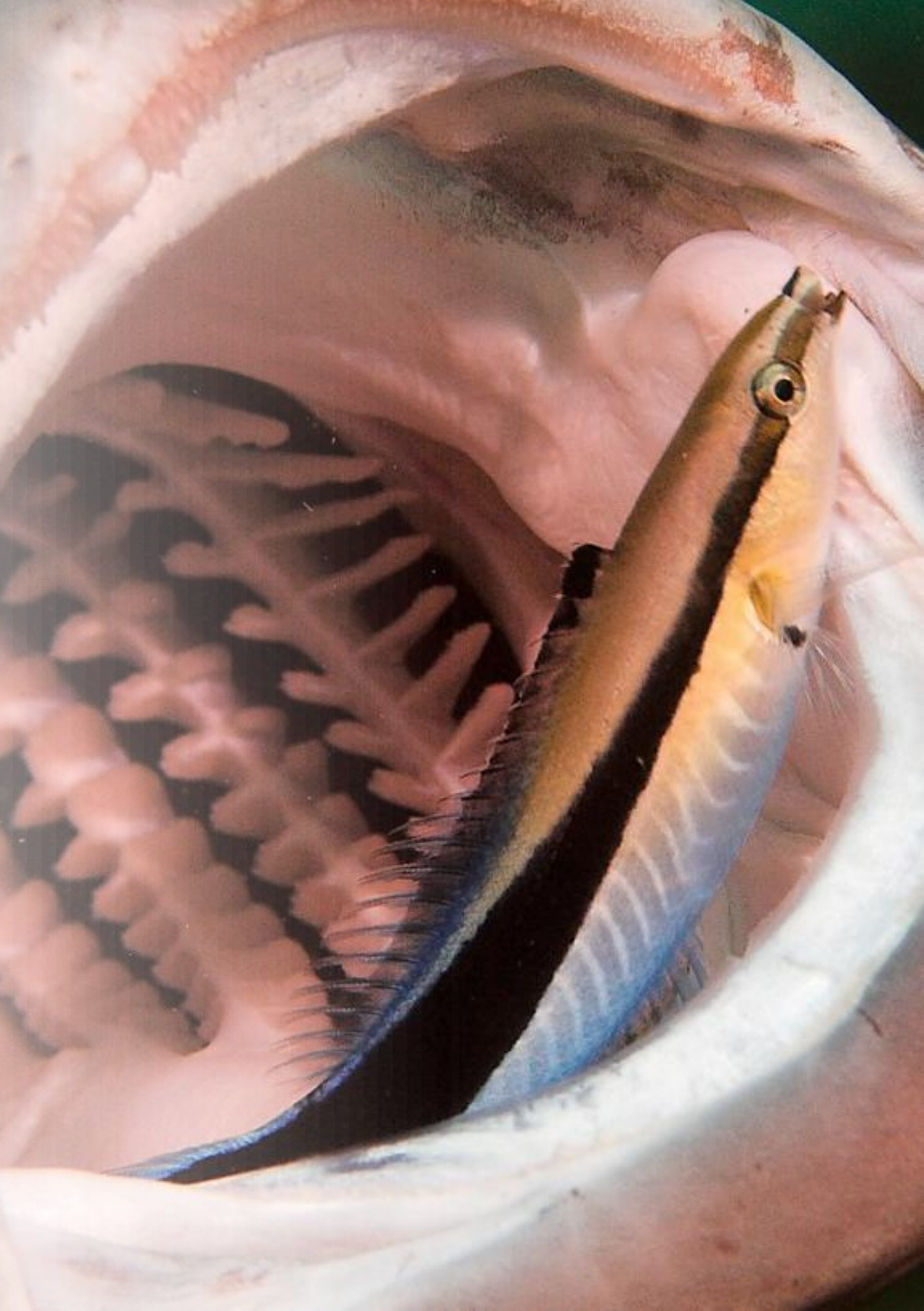
Why is it stable?

- **Partner choice and reputation**: clients can abandon cheating cleaners and seek out cooperative ones. Good cleaners attract more clients — their **reputation spreads** through the reef community.
- **Immediate retaliation**: clients can **"jolt"** or flee if bitten, ending the interaction immediately — a direct cost to the cheater.
- **Market effects**: at cleaning stations with multiple cleaners, clients preferentially visit the most cooperative ones, creating **competitive pressure** for honest service.
- **Tactile stimulation**: cooperative cleaners often **"massage"** clients with their fins, providing additional service that reinforces the relationship.



What game does it remind you?
And in terms of evolution of cooperation?

- This maps beautifully onto a **repeated prisoner's dilemma with reputation** — cooperation is maintained not by altruism but by the **shadow of future interactions**.
- Cheating provides immediate gain but destroys future opportunities, so cooperative cleaners outcompete cheaters in the long run.
- The system occasionally breaks down when cleaners do bite clients, especially juveniles still learning the strategy, but the multi-layered enforcement mechanisms (partner choice + reputation + immediate punishment) keep most interactions cooperative.



Ant agriculture

Approximately 66 million years ago, ants began cultivating their own food by entering into mutualisms with certain species of fungi and tending “fungal gardens”(Mueller and Rabeling 2008).

- Mutualism:
  - **Growing:**

    Ants promote the growth of the fungi, while eating some of the vegetative mycelium —threadlike hyphae that absorb nutrients from the soil and break down plant material—produced by their fungal partners.

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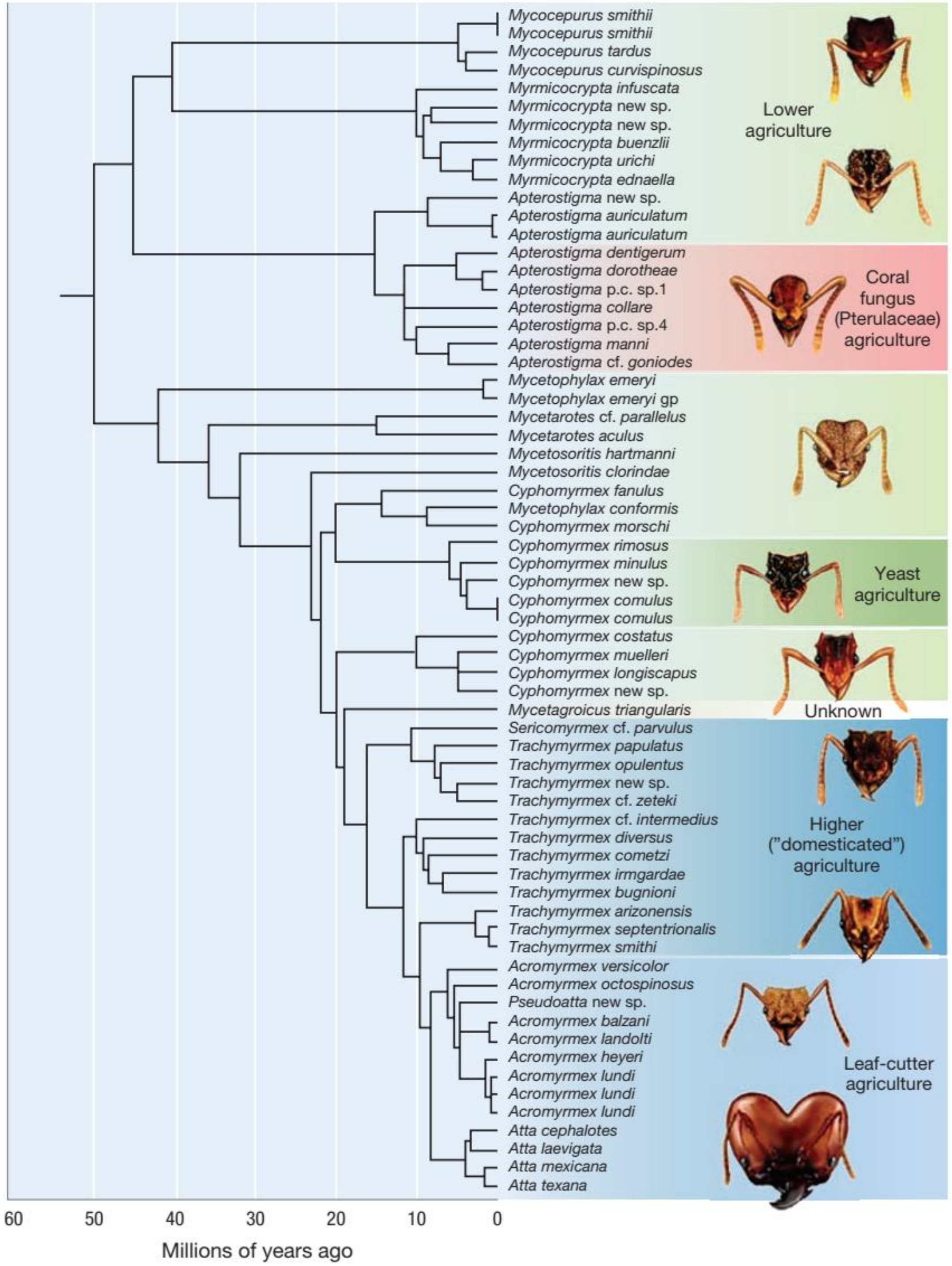

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- Mutualism:
  - **Growing:**

    Ants promote the growth of the fungi, while eating some of the vegetative mycelium —threadlike hyphae that absorb nutrients from the soil and break down plant material—produced by their fungal partners.
  - **Avoiding pathogens**:

    Attine ants such as the leaf-cutter ant *Acromyrmex octospinosus* and other fungal gardening ant species such as *Cyphomyrmex costatus* and *Apterostigma pilosum* (Currie et al. 1999a,b; Cafaro and Currie 2005; Mangone and Currie 2007;) not only grow but also **protect the fungi from disease**.

    Ants carry ***Streptomyces* bacteria** associated with them; these bacteria produce **antibiotics** that inhibit only *certain* parasitic diseases that directly threaten the fungal crop (specific against fungus *Escovopsis!)*.

    Vertical transmission of bacteria across generations, with parents—primarily mothers—passing the bacteria on to offspring;

    Some species of fungus-growing ants—but no other ant species—have specialized indentations known as **fovea** all over their bodies. The bacteria live in these fovea, and the fovea appear to be supplied with nutrients of some type by exocrine glands (Currie et al. 2006).

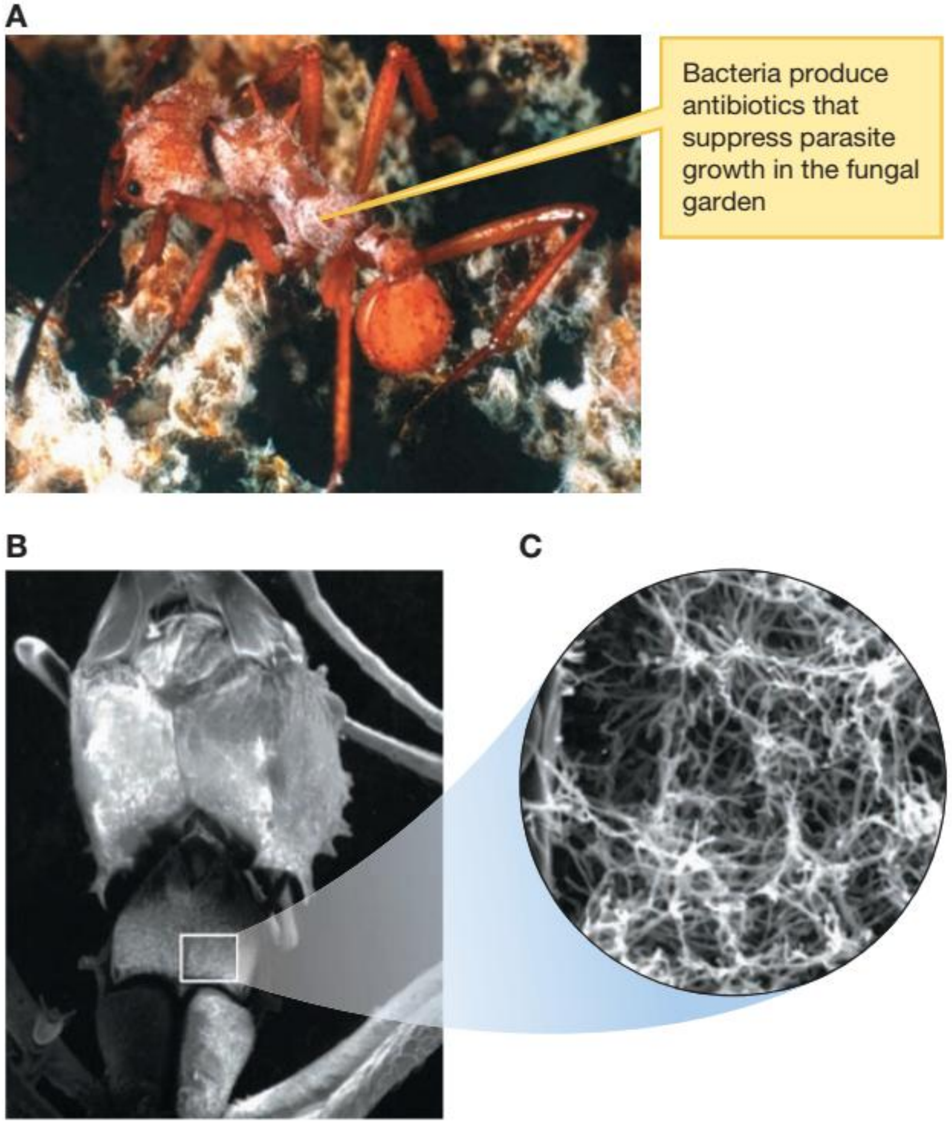


FIGURE 18.4 Leaf-cutter ants protect their fungal garden. **(A)** A worker of the leaf-cutter ant (*Acromyrmex octospinosus*) tending a fungal garden. The thick whitish-gray coating on the worker is composed of bacteria that produce the antibiotics that suppress the growth of parasites in the fungal garden. **(B)** Scanning electron micrograph of a worker, showing the location of the bacteria. **(C)** Detail of the micrograph in panel B.

Mutualistic networks often involve multiple partners

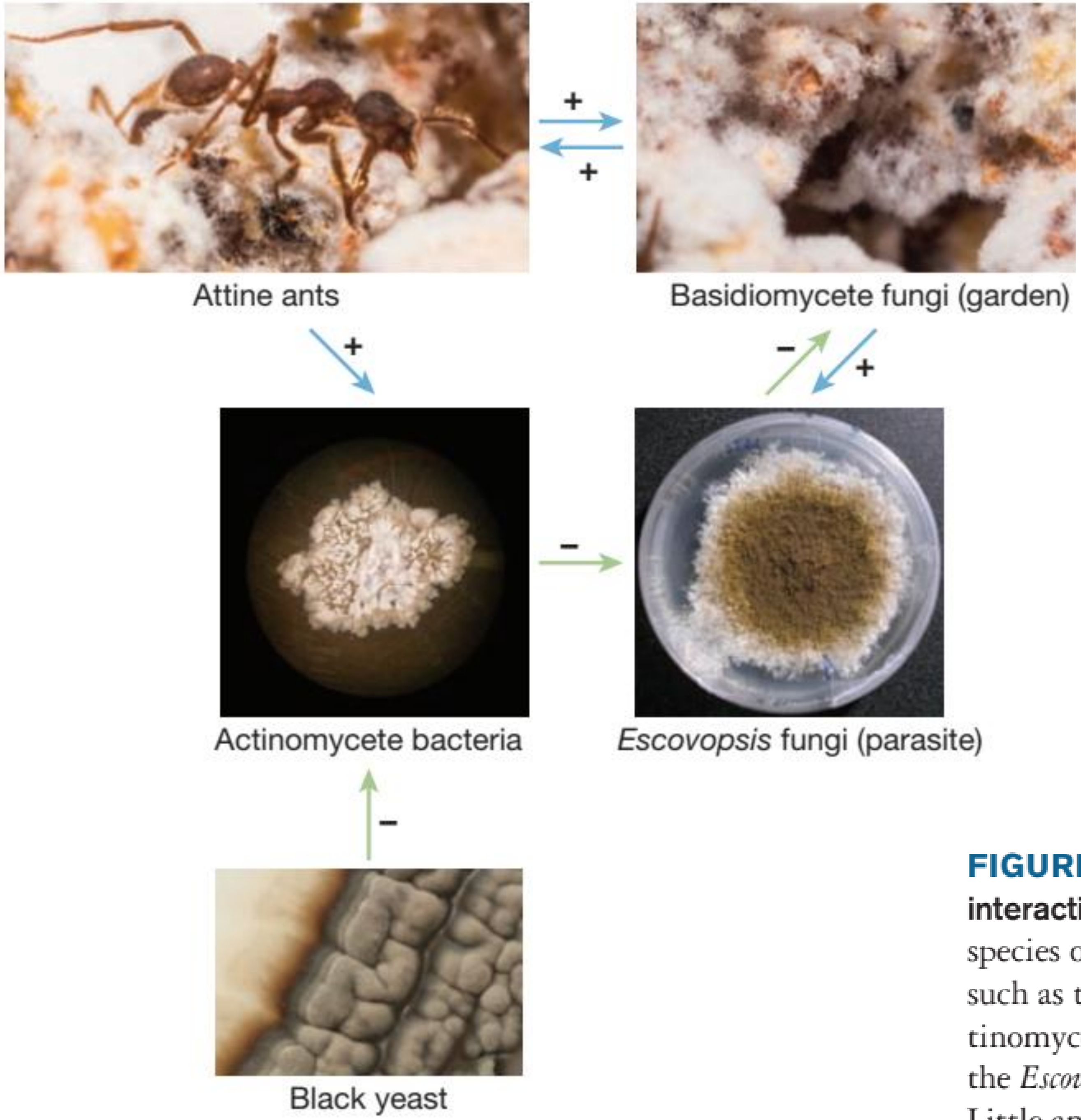
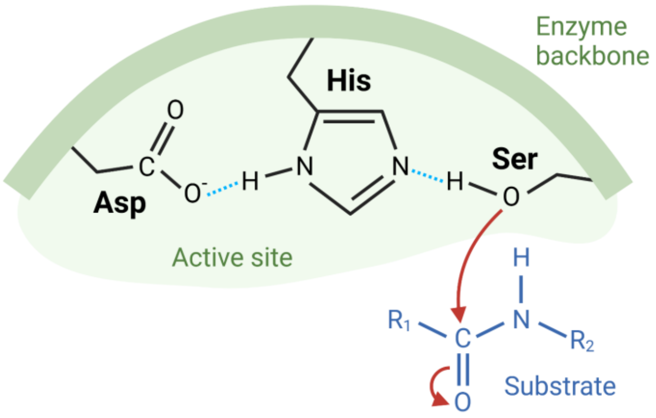


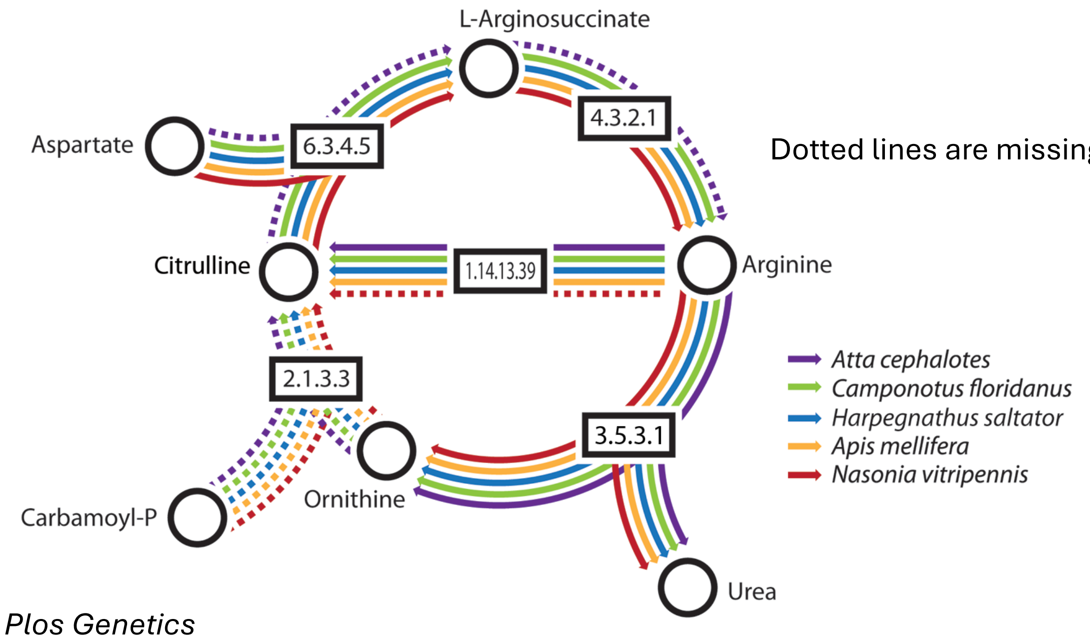
FIGURE 18.5 Five species are linked in a web of mutualistic interactions. Arrows indicate positive (+) or negative (–) direct effects of one species on another. There is an even more extensive web of indirect effects, such as the harmful effect that black yeast have on ants by feeding on the actinomycete bacteria (*Pseudonocardia* and *Streptomyces*) that help the ants exclude the *Escovopsis* parasite from their basidiomycete fungal gardens. Adapted from Little and Currie (2008).

Gene loss in some farmer ants

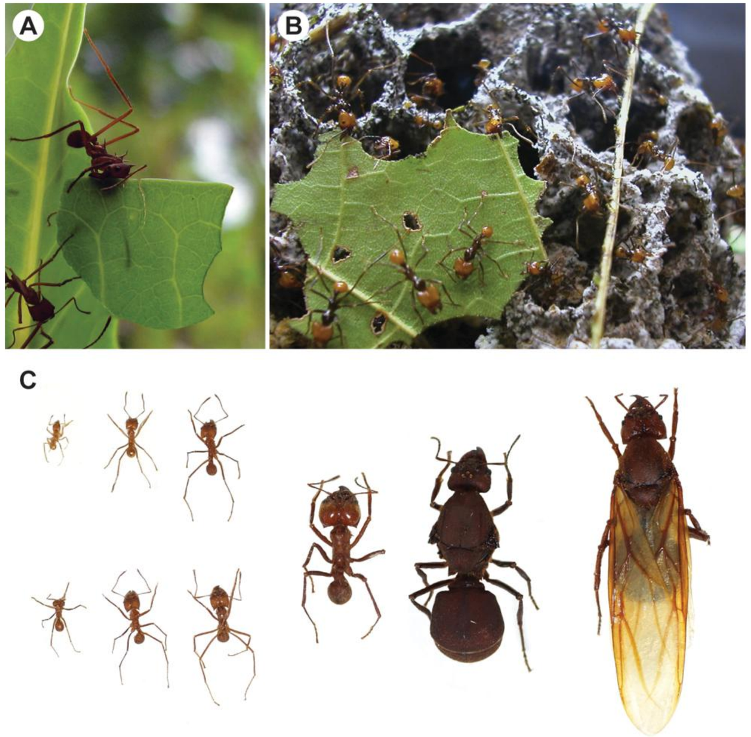
Leaf-cutter genomes would show evidence for the loss of genes associated with nutrient acquisition and normal digestion. For example *Atta cephalotes* – that relies on fungal gardens – shows extensive reduction in the production of enzymes serine proteases and producing the amino acid arginine (Suen et al. 2011)

Mechanism of Serine Protease

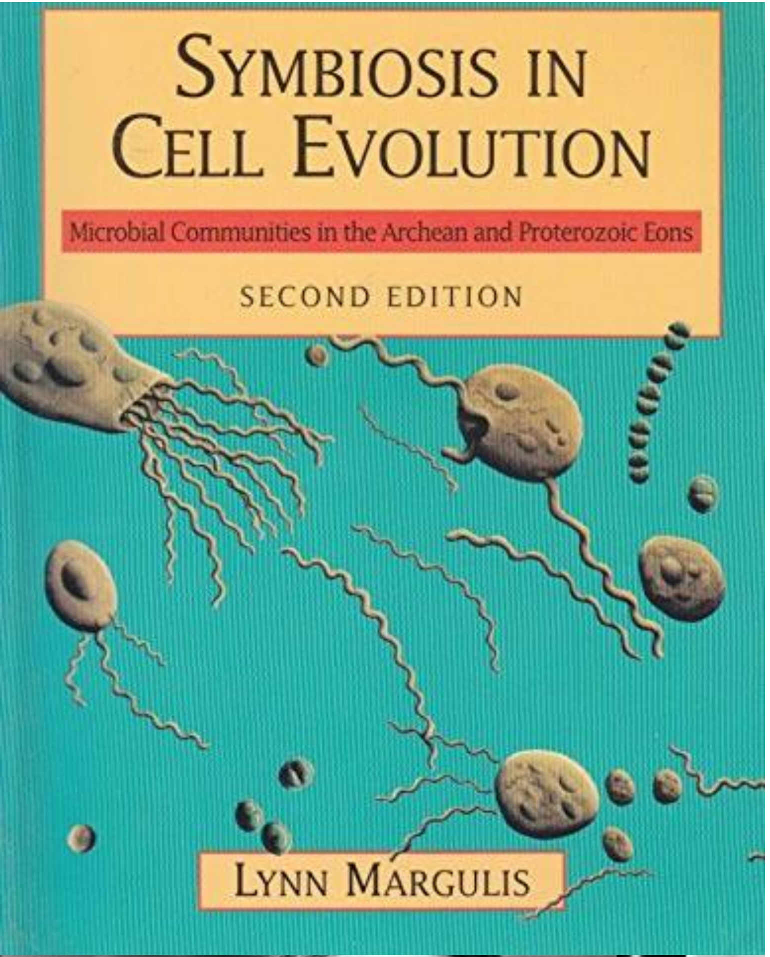




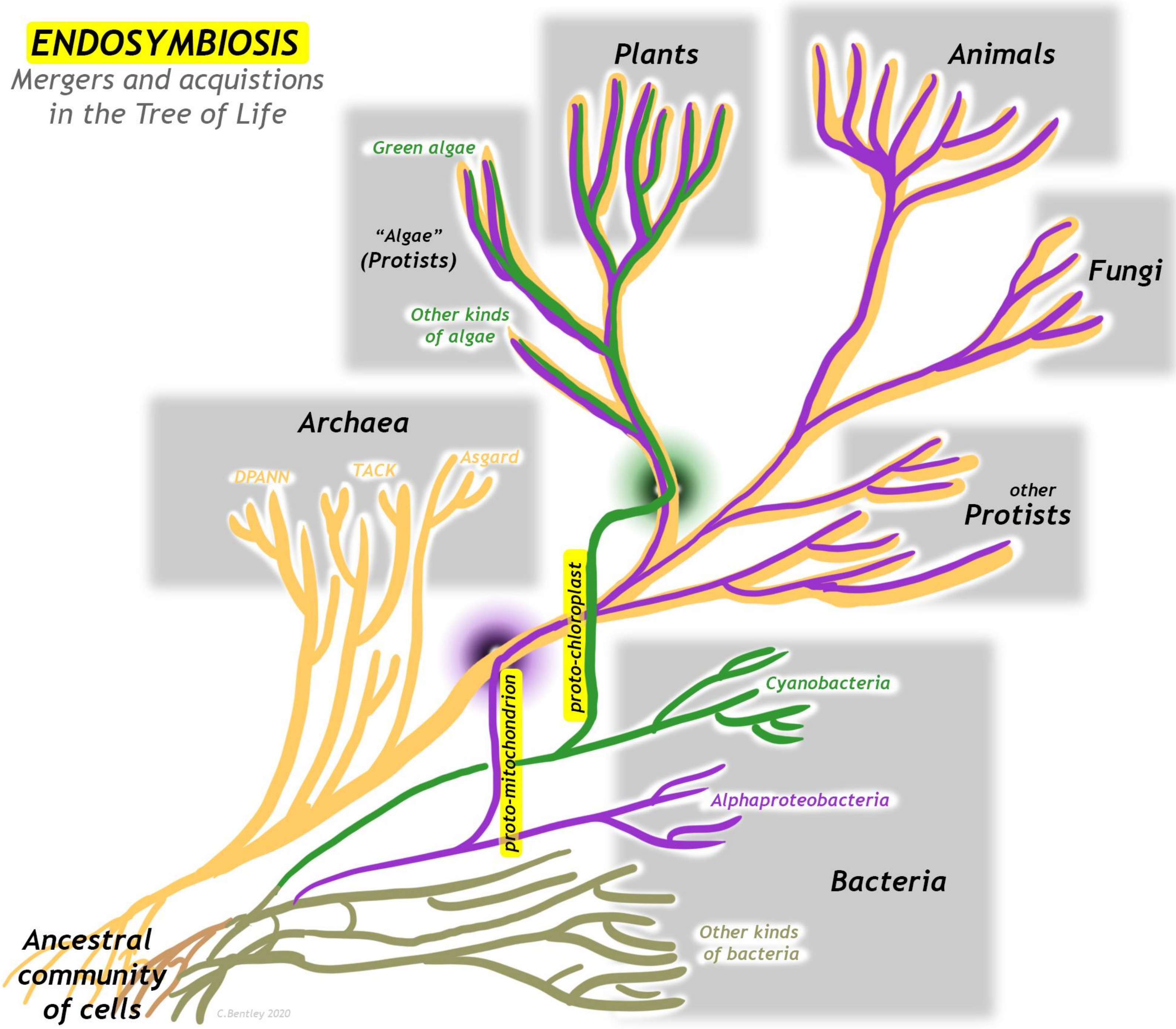
Dotted lines are missing in that species

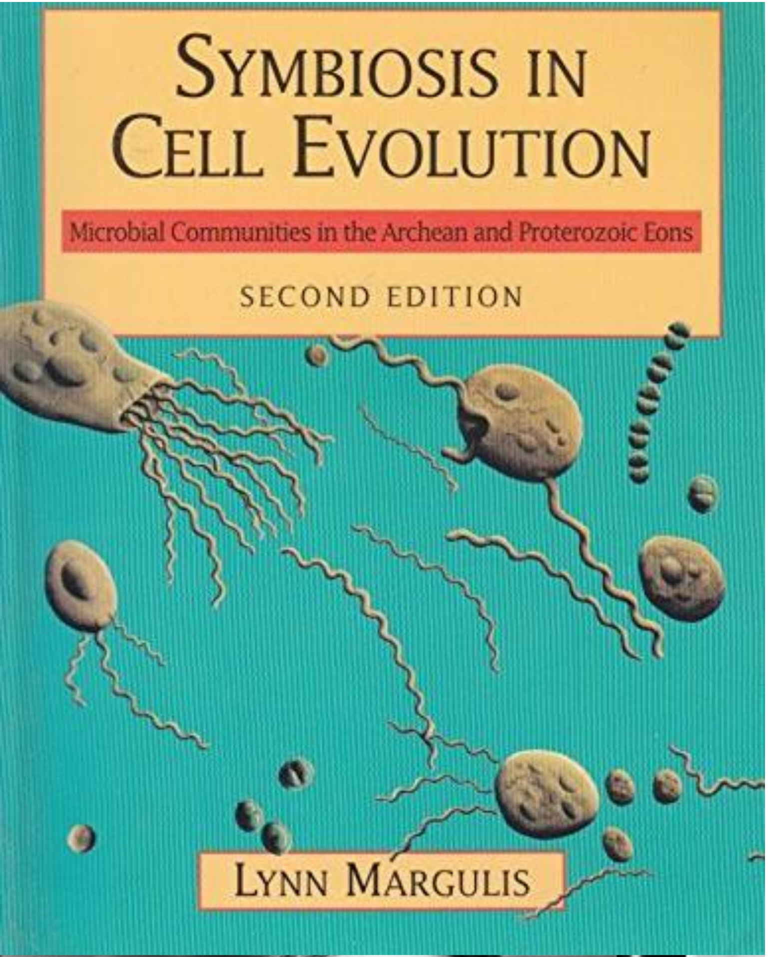


Suen et al. 2011, *Plos Genetics*



Lynn Margulis (1938 – 2011)





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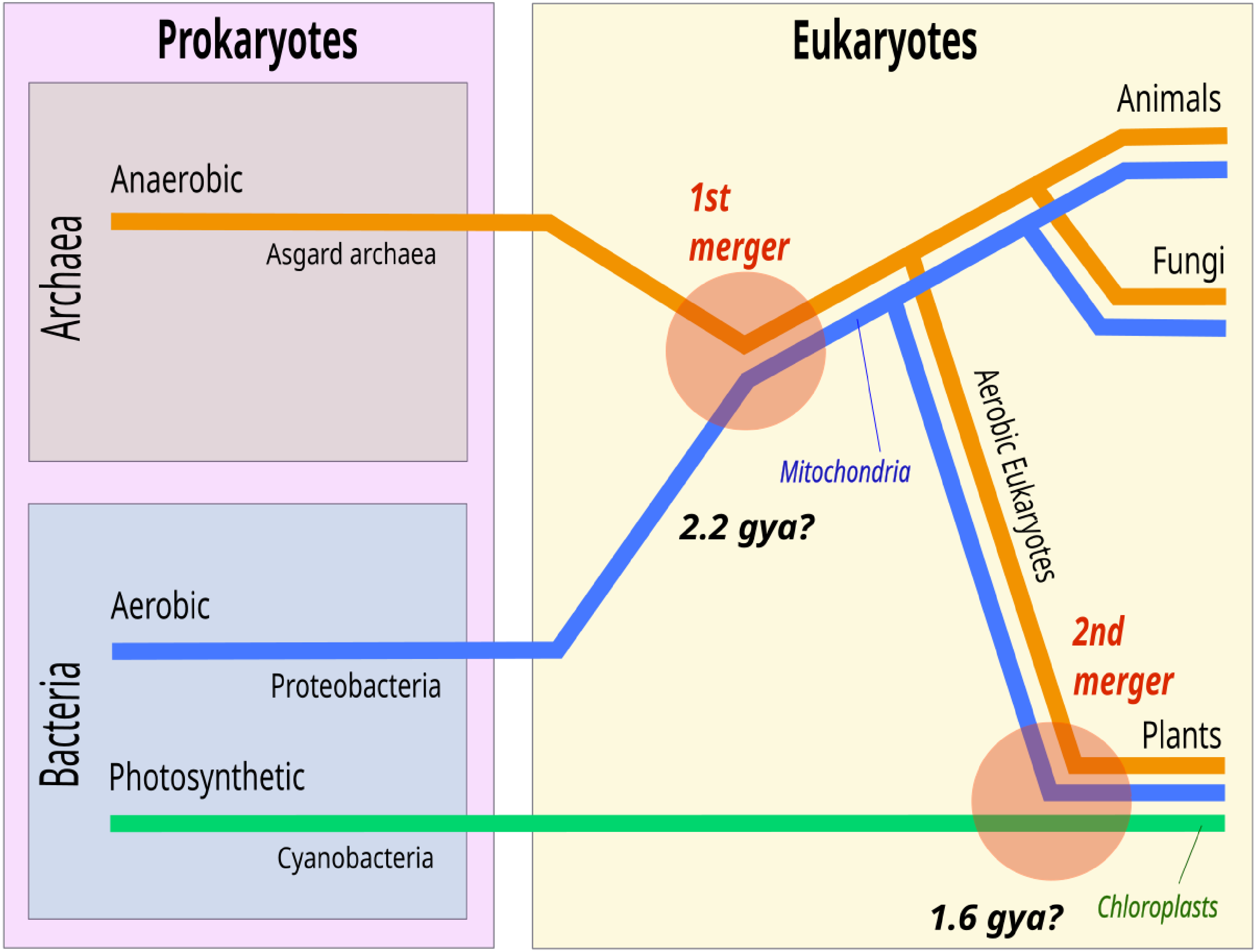
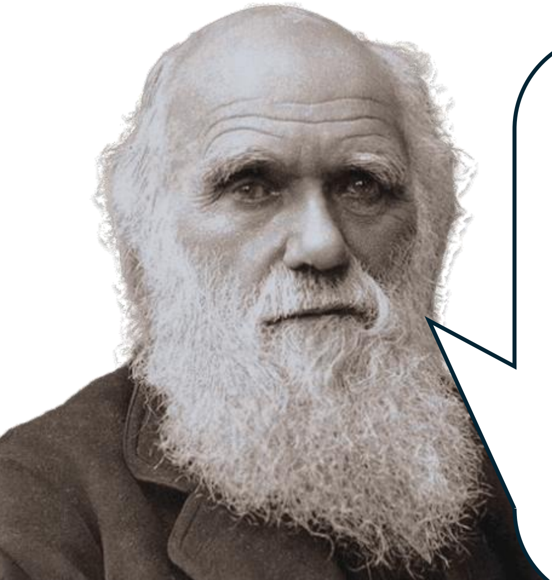


Yuccas: from «(seed) predators» to specialized mutualists

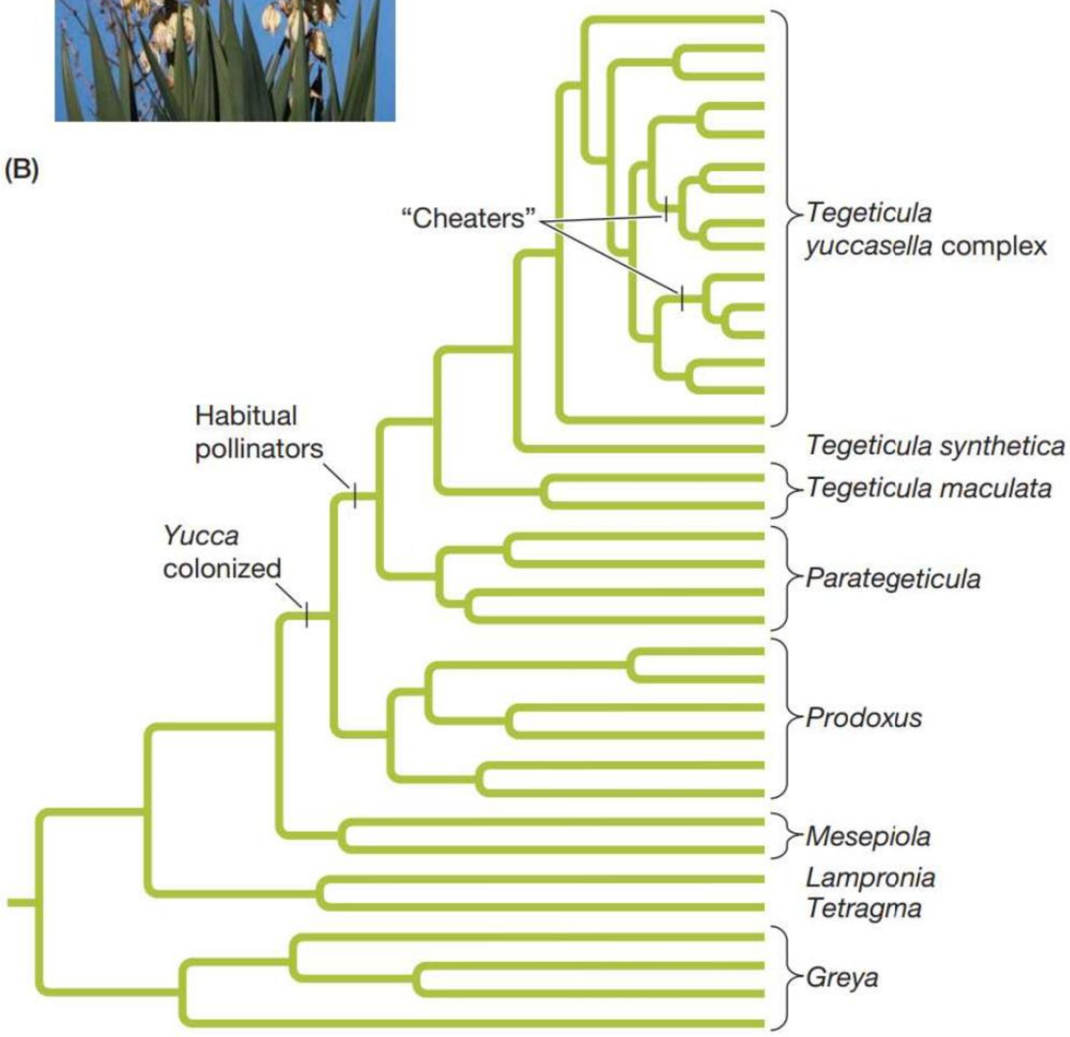
- Yuccas are pollinated only by female yucca moths (*Tegeticula* and *Parategeticula*), which carefully pollinate a yucca flower and then lay eggs in it. *Tegeticula also specialized mouthparts for active pollination (see fig).*
- The genera other than the "habitual pollinators" *Parategeticula* and *Tegeticula* are seed predators.
- Likely mutualism evolved from "predation".



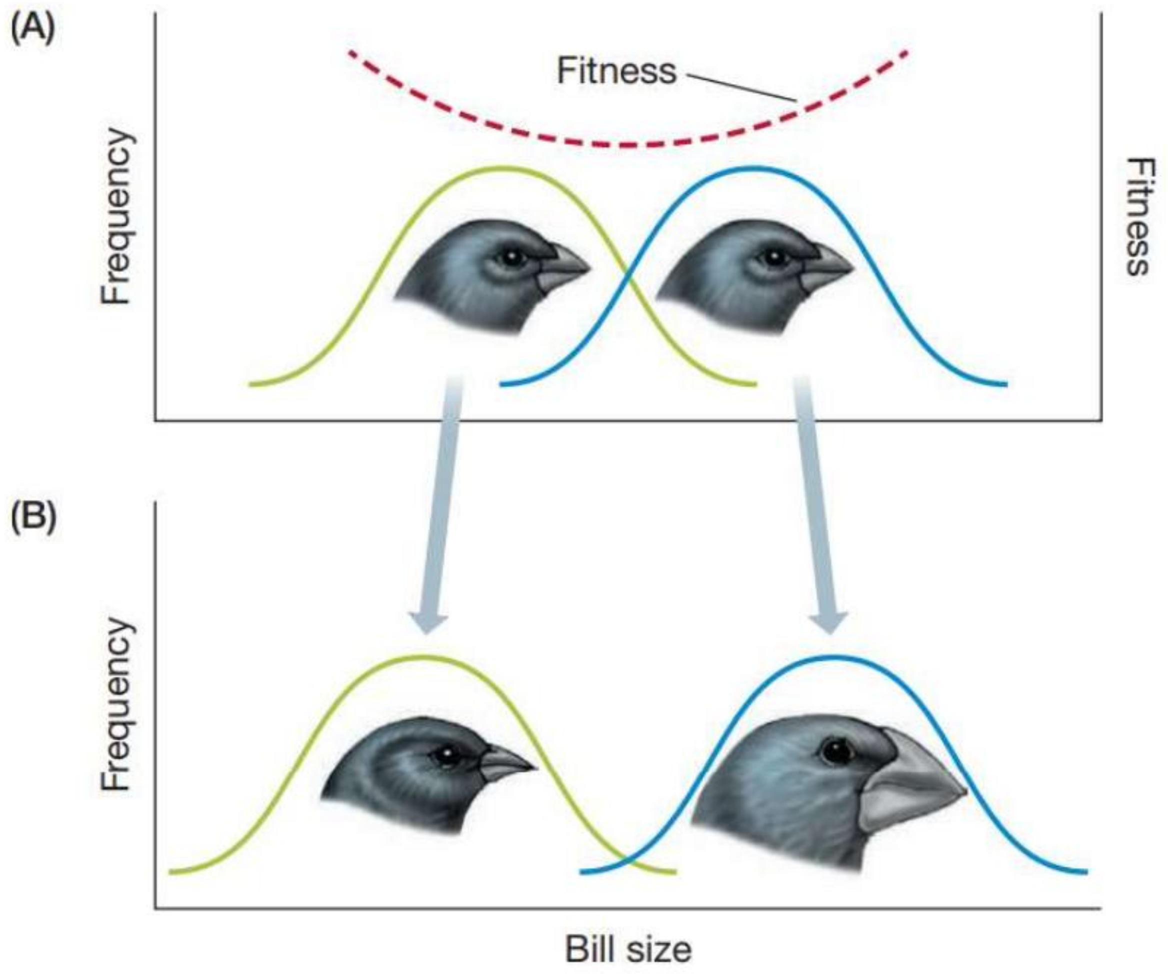
I challenge anyone to find an instance of a species having been modified solely for the benefit of another species, "for such could not have been produced through natural selection."
On the Origin of SPecies

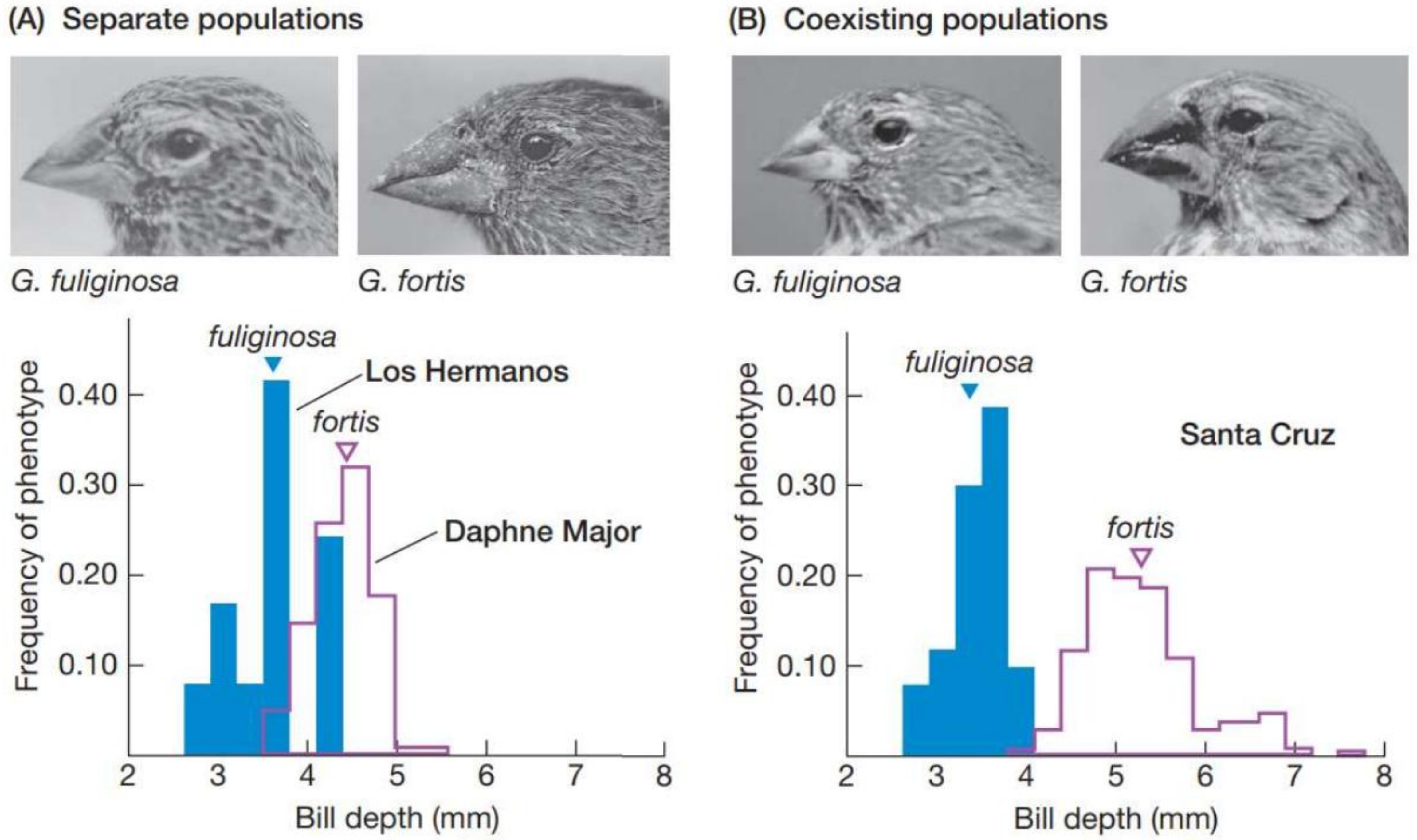
(A)

(B)

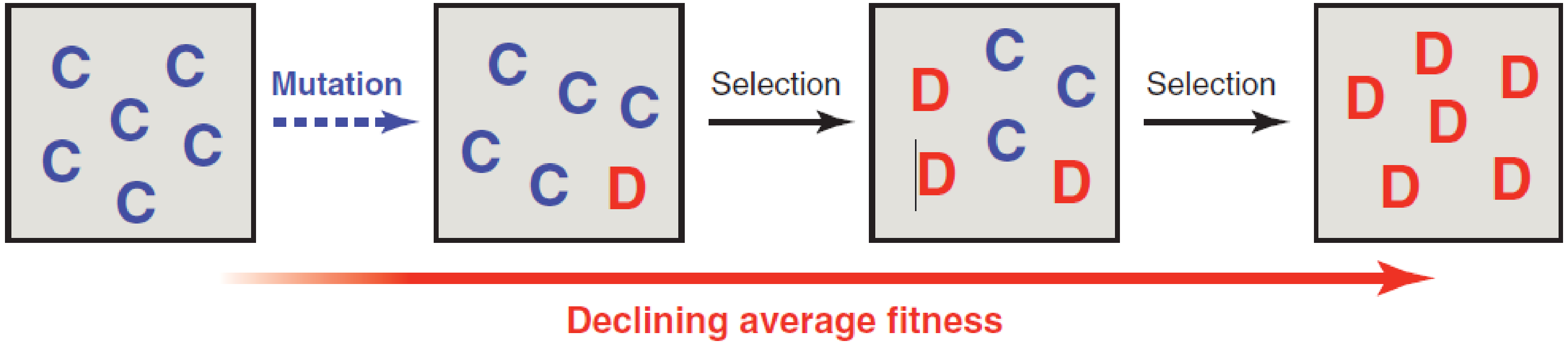


Competition favors divergence in characters




(A) Separate populations
G. fuliginosa
G. fortis
fuliginosa
Los Hermanos
fortis
Daphne Major
Frequency of phenotype
0.40
0.30
0.20
0.10
2
3
4
5
6
7
8
Bill depth (mm)
(B) Coexisting populations
G. fuliginosa
G. fortis
fuliginosa
Santa Cruz
fortis
Frequency of phenotype
0.40
0.30
0.20
0.10
2
3
4
5
6
7
8
Bill depth (mm)

The Prisoner's dilemma is a «strict» social dilemma where it is always convenient to defect



	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
D (Defect)	b	0

b=benefit provided by the cooperator
c=cost of cooperation

Prisoner's dilemma and the tragedy of common

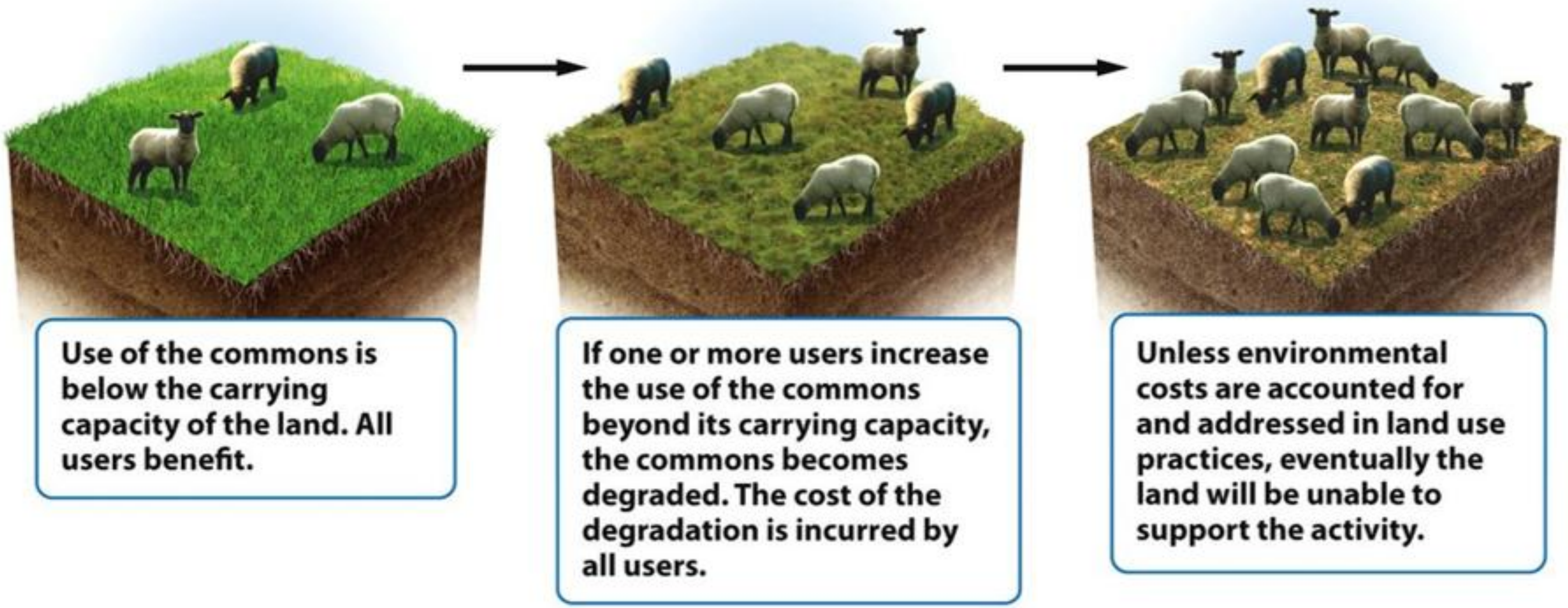
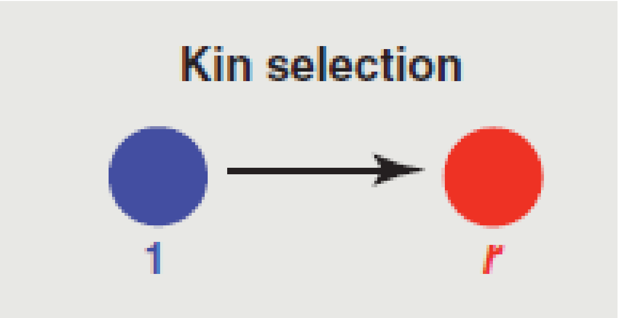


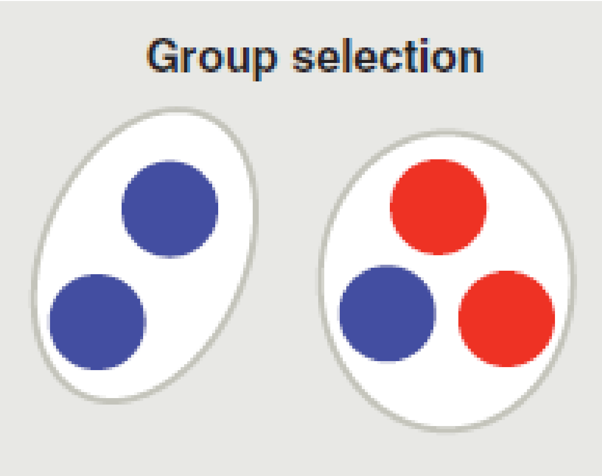
Figure 10.2
Environmental Science
© 2012 W. H. Freeman and Company

Fives rules for the evolution of cooperation

Martin Nowak, 2006, Nature

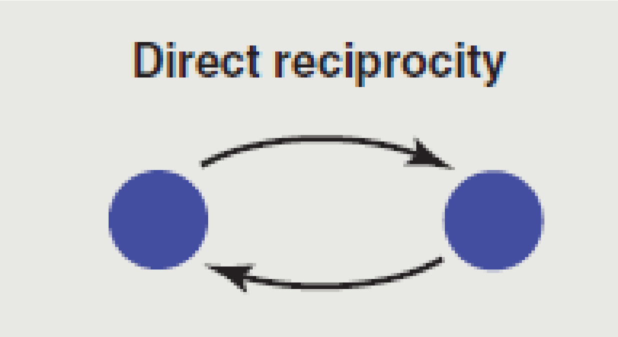
Related individuals



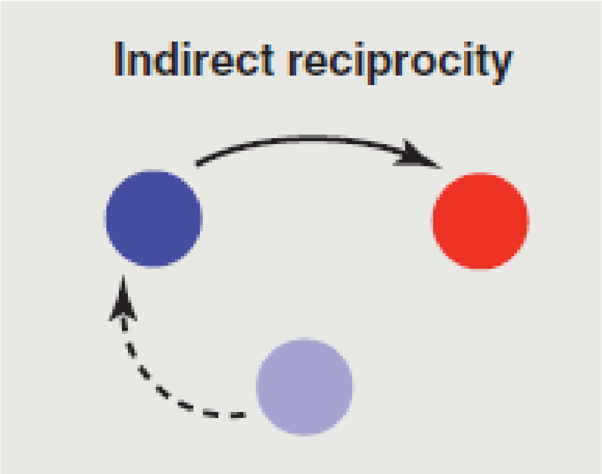


Individuals in groups

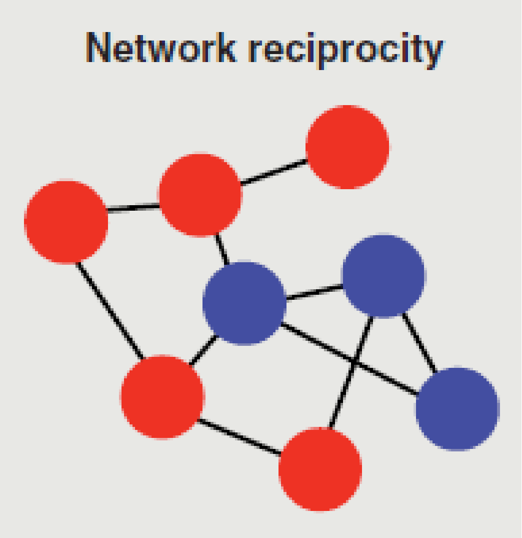
Repeated interactions



Reputation

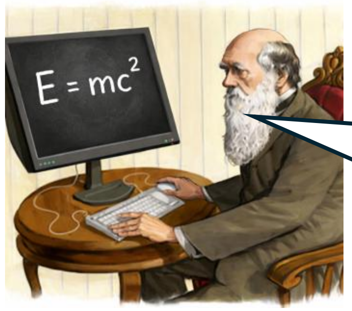


Cooperators Defectors



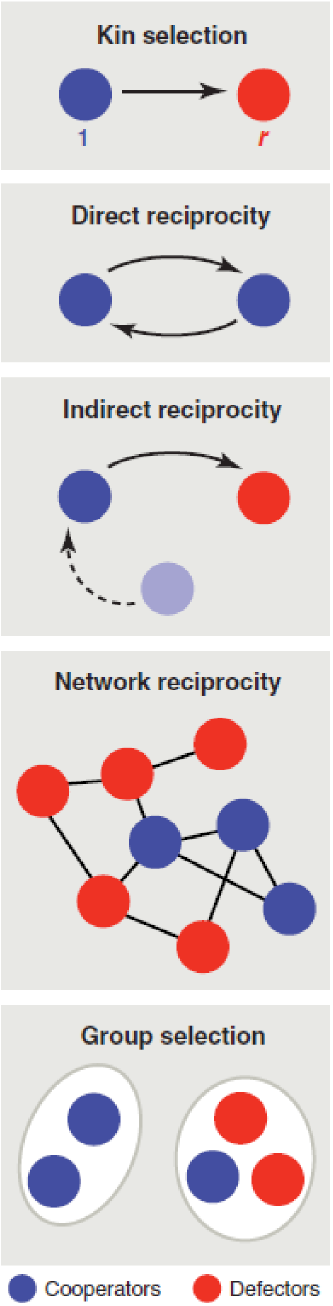
Interactions in space

Fives rules for the evolution of cooperation



Try to derive Hamilton's rule using Game Theory and the same approach we used for Hawks and Doves!

Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$	r…genetic relatedness
	D	$b-rc$	0		
Direct reciprocity	C	$(b-c)/(1-w)$	$-c$	$\frac{b}{c} > \frac{1}{w}$	w…probability of next round
	D	b	0		
Indirect reciprocity	C	$b-c$	$-c(1-q)$	$\frac{b}{c} > \frac{1}{q}$	q…social acquaintanceship
	D	$b(1-q)$	0		
Network reciprocity	C	$b-c$	$H-c$	$\frac{b}{c} > k$	k…number of neighbors
	D	$b-H$	0		
Group selection	C	$(b-c)(m+n)$	$(b-c)m-cn$	$\frac{b}{c} > 1+\frac{n}{m}$	n…group size; m…number of groups
	D	bn	0		



Exercise: deriving Hamilton's rule

Payoff matrix

		C	D	ESS
Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$
	D	$b-rc$	0	

- W_C=?
- W_D=?

Exercise: deriving Hamilton's rule

Payoff matrix

		C	D	ESS
Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c}>\frac{1}{r}$
	D	$b-rc$	0	

- $W_C=p(b-c)(1+r)+(1-p)(br-c)$
- $W_D=pb-prc$

- Let's find out when C is an Evolutionarily Stable Strategy?

  $W_C>W_D$

Exercise: deriving Hamilton's rule

Payoff matrix

		C	D	ESS
Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$
	D	$b-rc$	0	

- $W_C = p(b-c)(1+r)+(1-p)(br-c)$
- $W_D = pb-prc$

- Let's find out when C is an Evolutionarily Stable Strategy?

  $W_C > W_D$

The general structure of 2-players' games

	A	B
A	a	b
B	c	d

$$f_A = a x_A + b x_B$$ Fitness of strategy A

$$f_B = c x_A + d x_B$$ Fitness of strategy B

The general structure of 2-players' games

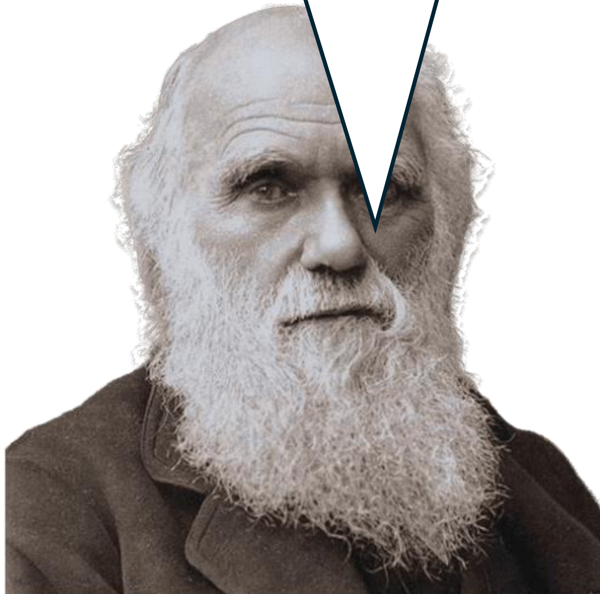
	A	B
A	a	b
B	c	d

$f_A = a x_A + b x_B$ Fitness of strategy A

$f_B = c x_A + d x_B$ Fitness of strategy B

$\phi = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$ Average fitness

Now let's just say that the frequency of A (x_A) increases if its fitness is higher than the average fitness (and viceversa)



The general structure of 2-players' games

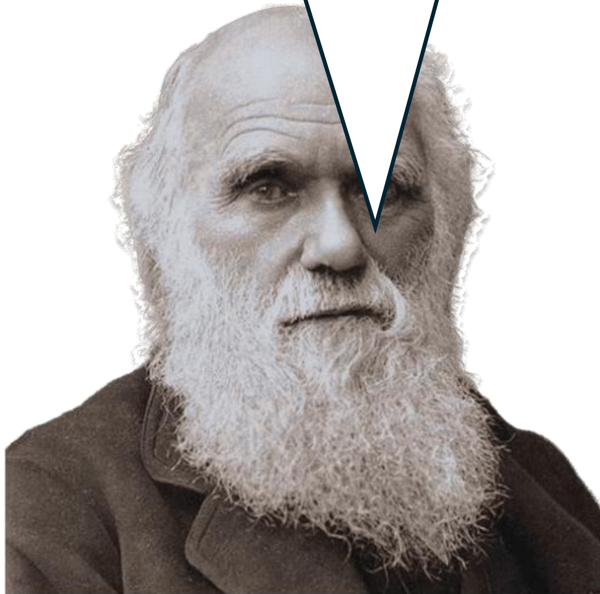
	A	B
A	*a*	*b*
B	*c*	*d*

$$[f_A(\vec{x}) - \phi] \uparrow$$

$$\downarrow$$

$$x_A \uparrow$$

Now let's just say that the frequency of A (x_A) increases if its fitness is higher than the average fitness (and viceversa)



$$f_A = ax_A + bx_B$$ Fitness of strategy A

$$f_B = cx_A + dx_B$$ Fitness of strategy B

$$\phi = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$$ Average fitness

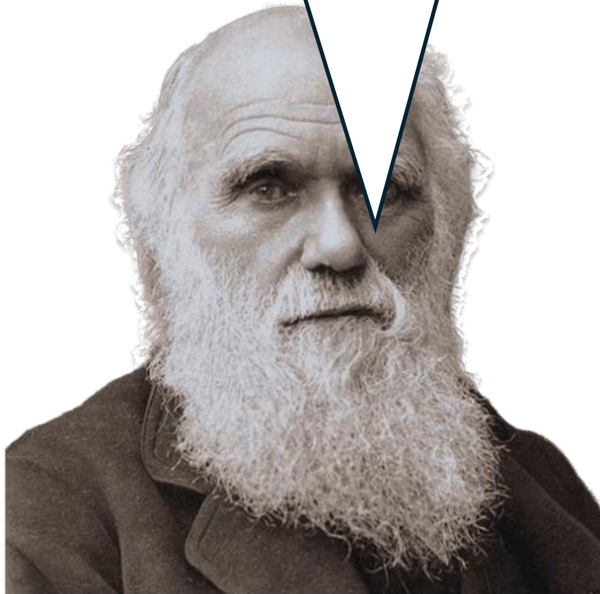
The general structure of 2-players’ games

	A	B
A	a	b
B	c	d

Change in frequency of A — frequency of A — fitness of A — Average fitness

$$\dot{x}_A = x_A[f_A(\vec{x}) - \phi]$$

Now let’s just say that the frequency of A (x_A) increases if its fitness is higher than the average fitness (and viceversa)



$$f_A = ax_A + bx_B$$ Fitness of strategy A

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$$\phi = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$$ Average fitness

The general structure of 2-players' games

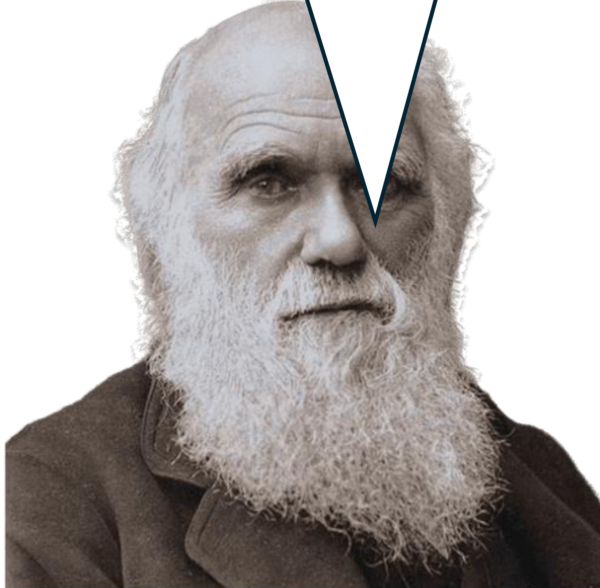
	A	B
A	a	b
B	c	d

Change in frequency of A — frequency of A — fitness of A — Average fitness

$$\dot{x}_A = x_A[f_A(\vec{x}) - \phi]$$

$$\dot{x}_B = x_B[f_B(\vec{x}) - \phi]$$

Now let's just say that a population increase/decrease if higher/lower than the average fitness



The general structure of 2-players' games

	A	B
A	a	b
B	c	d

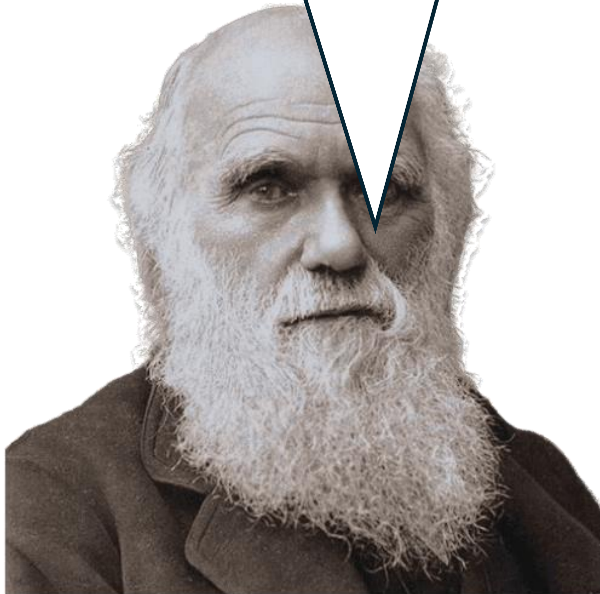
Change in frequency of A — frequency of A — fitness of A — Average fitness

$$\dot{x}_A = x_A[f_A(\vec{x}) - \phi]$$

$$\dot{x}_B = x_B[f_B(\vec{x}) - \phi]$$

Simplifying and taking
x=xA=1-xB

Now let's just say that a population increase/decrease if higher/lower than the average fitness



The general structure of 2-players' games

	A	B
A	a	b
B	c	d

Change in frequency of A — frequency of A — fitness of A — Average fitness

$$\dot{x}_A = x_A[f_A(\vec{x}) - \phi]$$

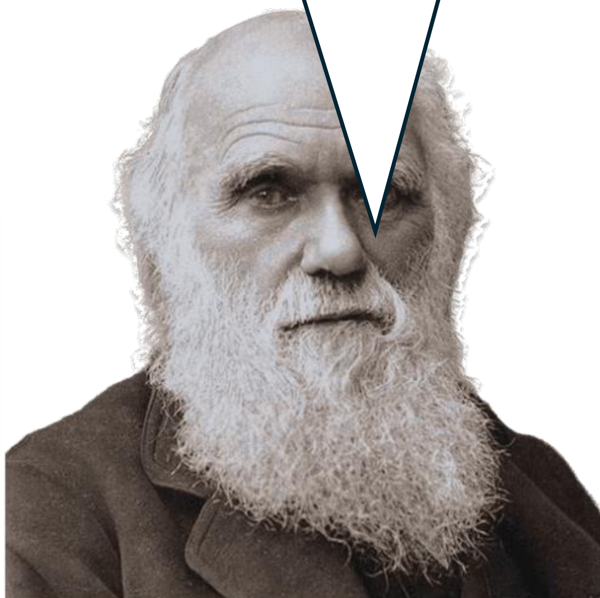
$$\dot{x}_B = x_B[f_B(\vec{x}) - \phi]$$

Simplifying and taking
x=xA=1-xB

$$\dot{x} = x(1-x)[(a-b-c+d)x+b-d].$$

Replicator's equation

Now let's just say that a population increase/decrease if higher/lower than the average fitness



The general structure of 2-players' games

	A	B
A	*a*	*b*
B	*c*	*d*

Change in frequency of A

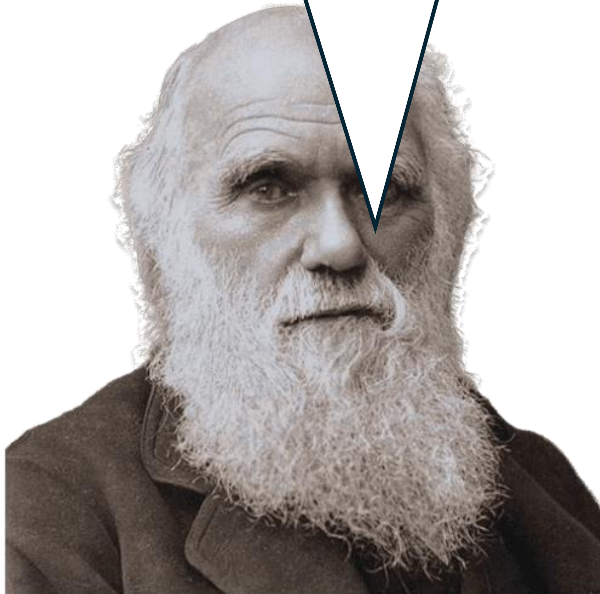
Frequency of A

Payoffs

$$\dot{x} = x(1 - x)[(a - b - c + d)x + b - d].$$

Replicator's equation

Now let's just say that a population increase/decrease if higher/lower than the average fitness



The general structure of 2-players' games

	A	B
A	*a*	*b*
B	*c*	*d*

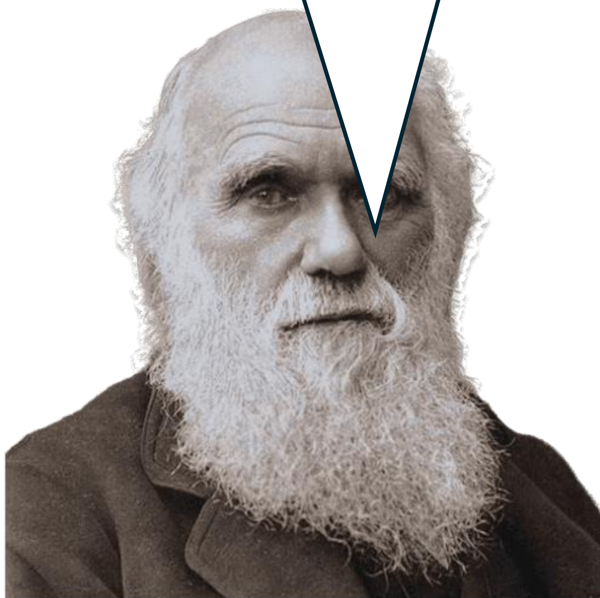
Now let's just say that a population increase/decrease if higher/lower than the average fitness

Do you recognize this?

Payoffs

$$\dot{x} = x(1 - x)[(a - b - c + d)x + b - d].$$

Replicator's equation



The general structure of 2-players' games

	A	B
A	*a*	*b*
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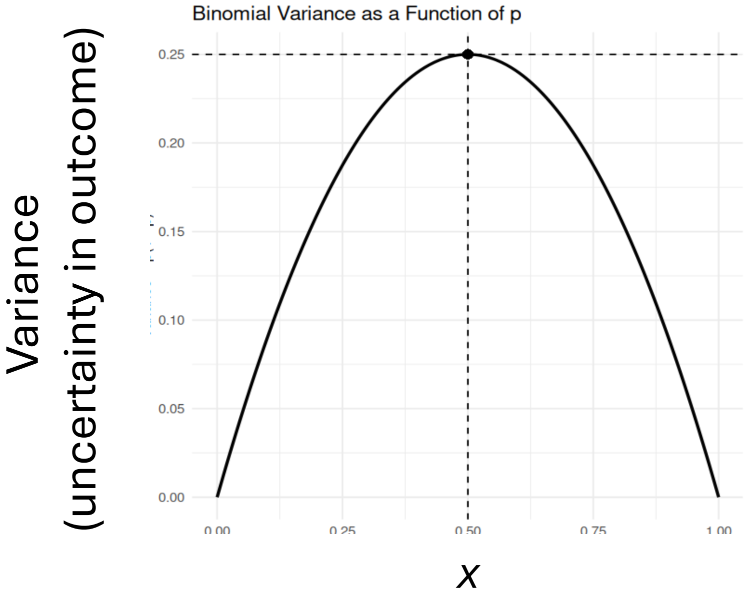
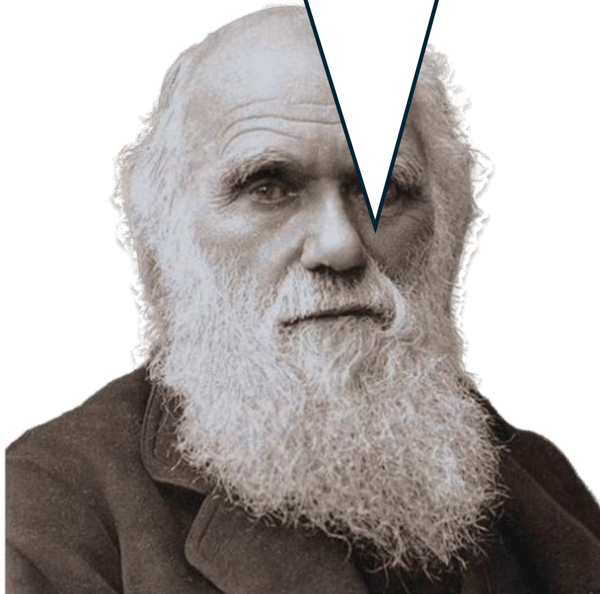


The variance of a Binomial Distribution is **p(1-p)**.



Do you recognize this?

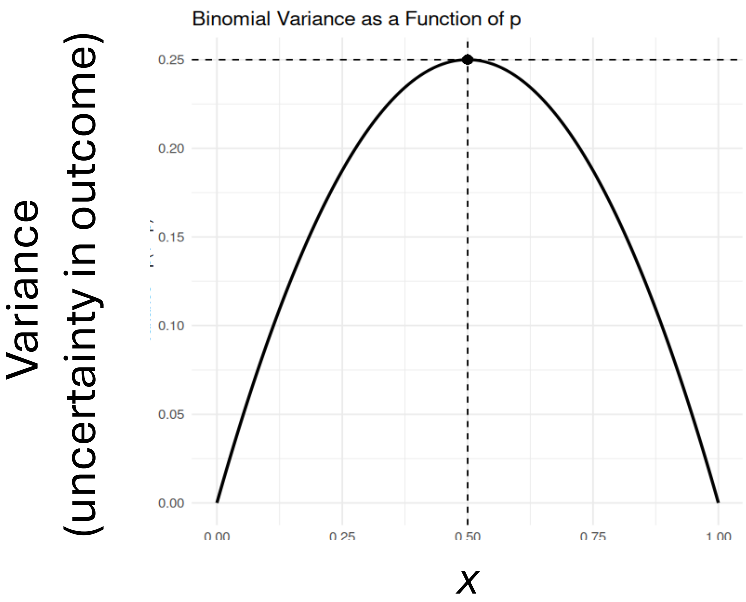
Payoffs

$$\dot{x} = x(1-x)[(a-b-c+d)x+b-d].$$

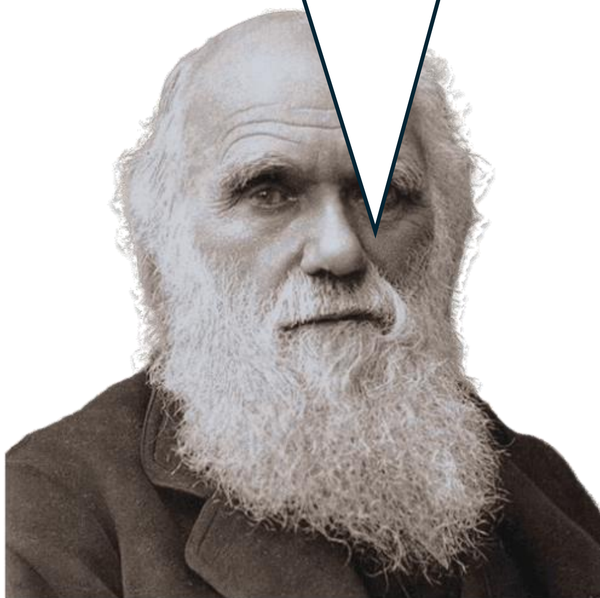
Replicator's equation

The general structure of 2-players' games

	A	B
A	a	b
B	c	d



Do not worry, we will do a short statistic recap in a couple of lectures



Do you recognize this?

Payoffs

$$\dot{x} = x(1-x)[(a-b-c+d)x+b-d].$$

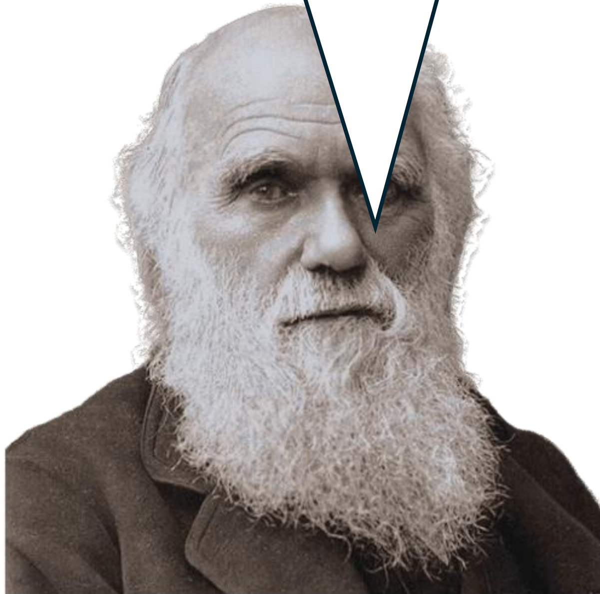
Replicator's equation

The general structure of 2-players’ games

	A	B
A	a	b
B	c	d

- **Variability among individuals**
- Differential contribution to successive generations
- Mechanism of inheritance

The stronger the variance, the faster evolution!



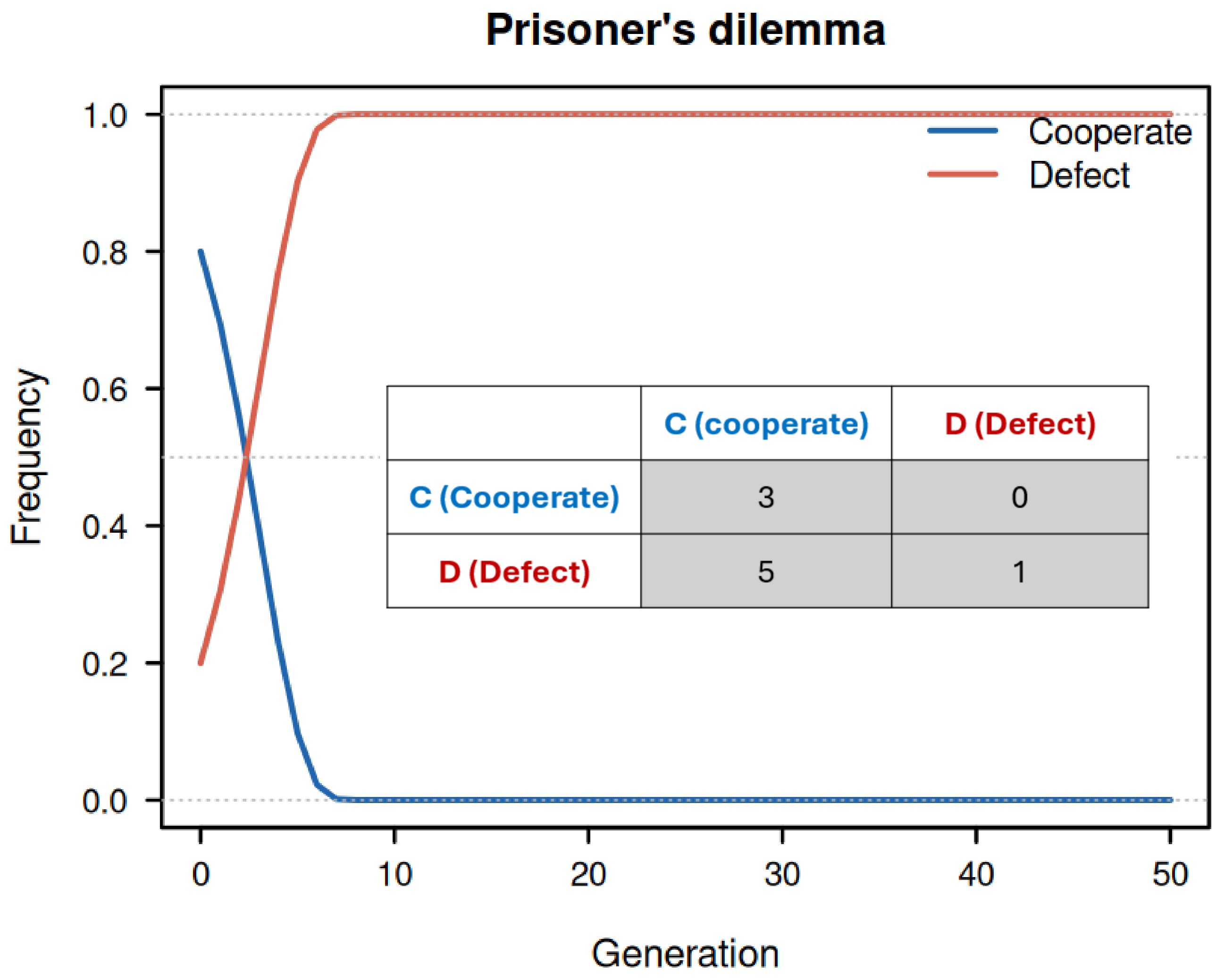
Variability in strategy in the population

Payoffs

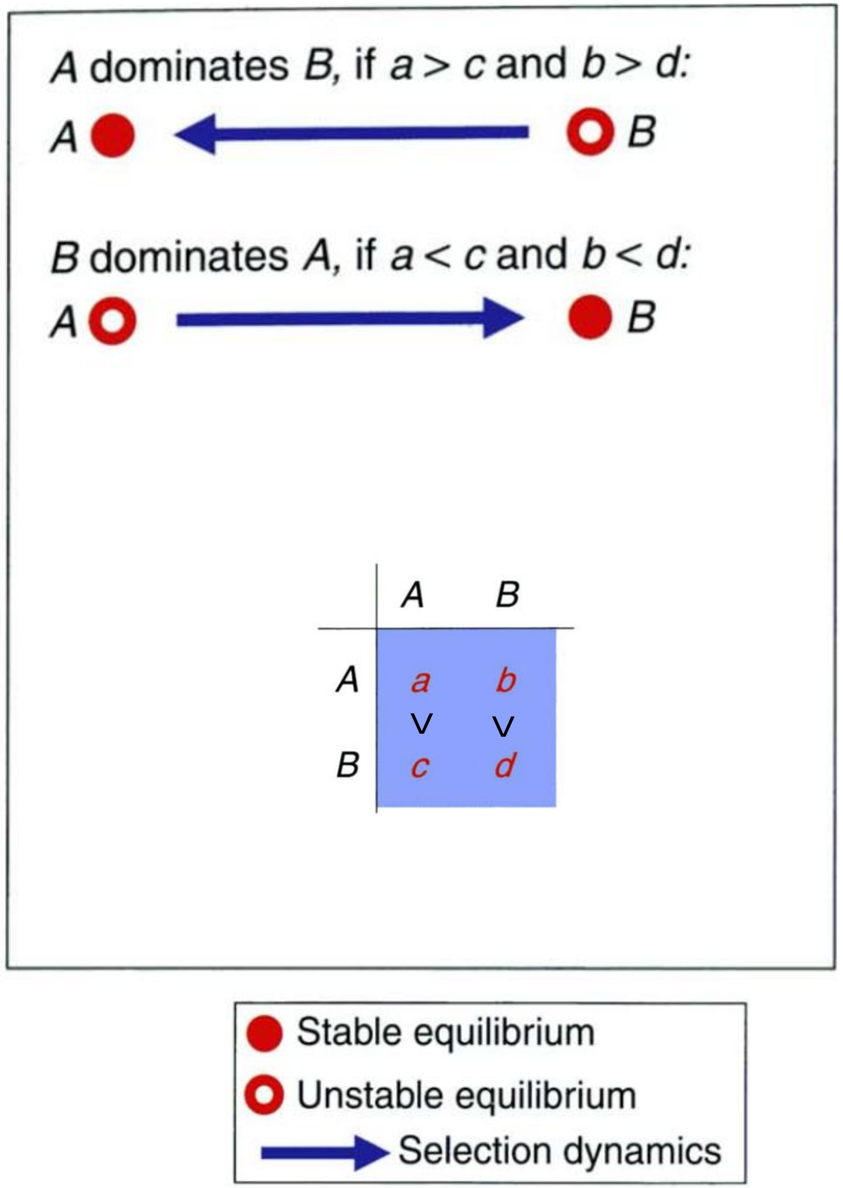
$$\dot{x} = x(1-x)[(a-b-c+d)x + b - d].$$

Replicator’s equation

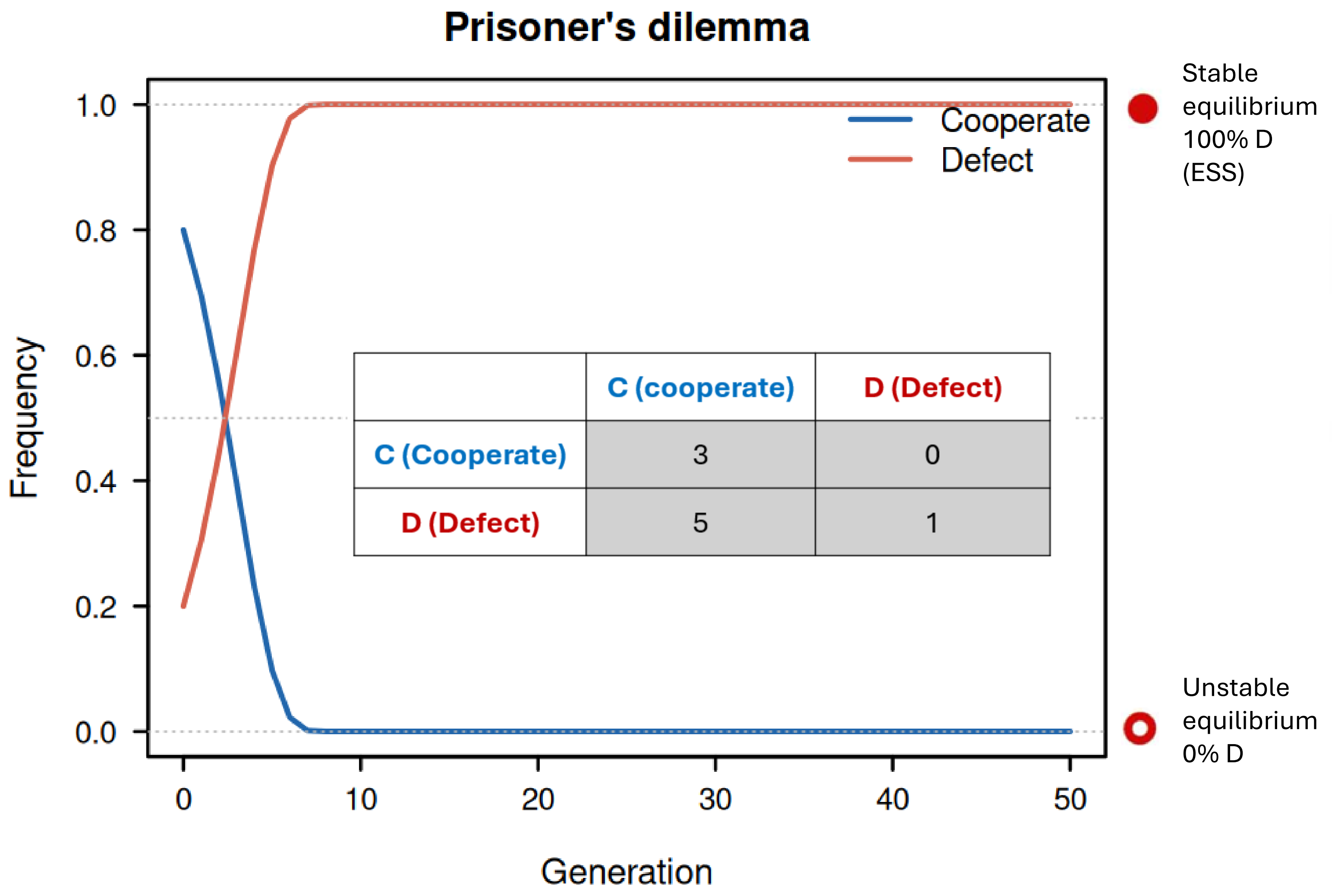
Evolutionary dynamics: Prisoner's dilemma



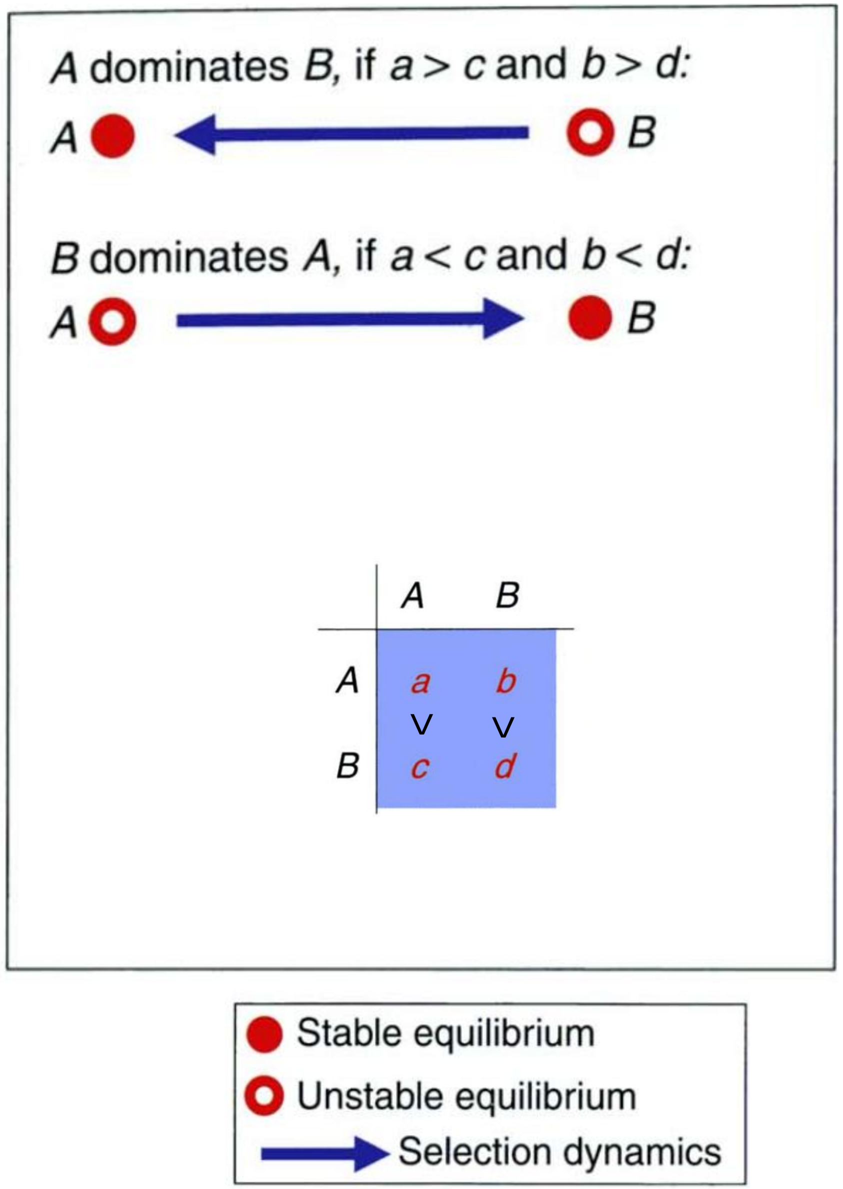
	C (cooperate)	D (Defect)
C (Cooperate)	3	0
D (Defect)	5	1



Evolutionary dynamics: Prisoner's dilemma



	C (cooperate)	D (Defect)
C (Cooperate)	3	0
D (Defect)	5	1



The general structure of 2-players' games

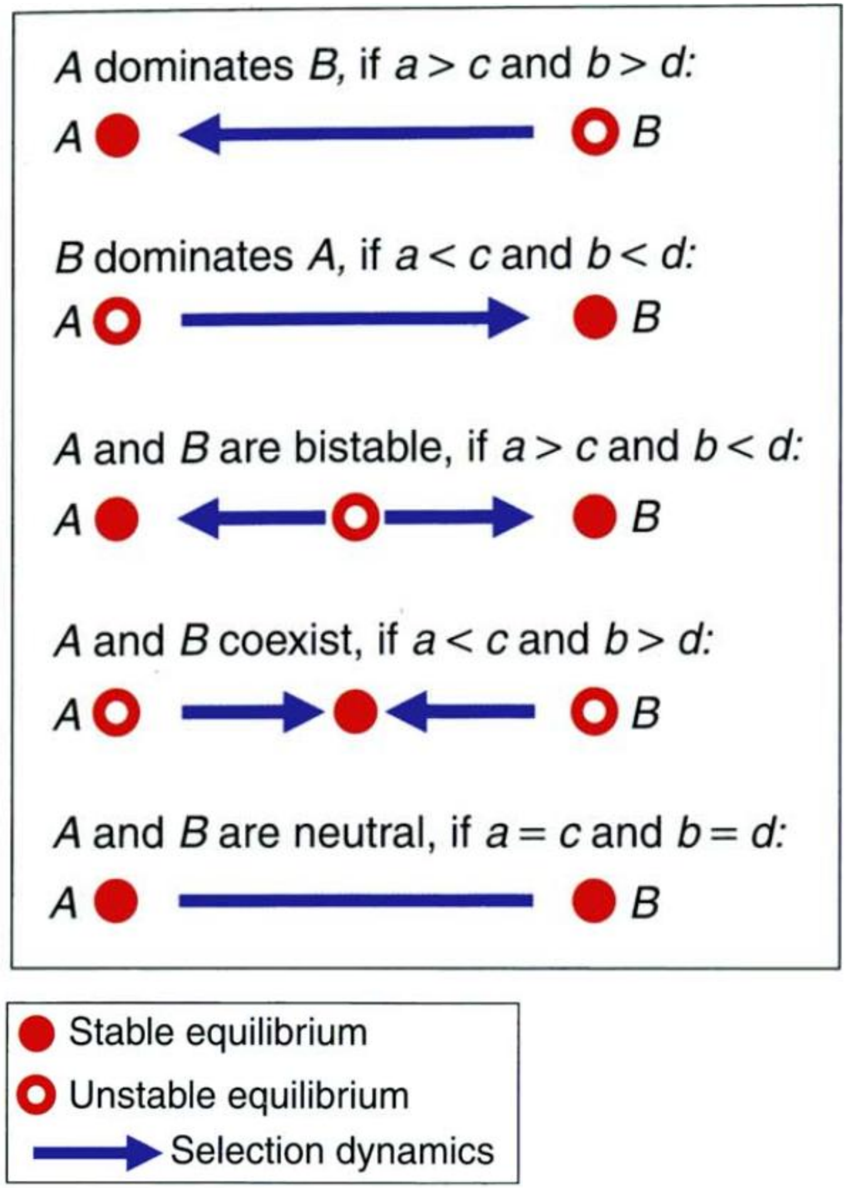
	A	B
A	a	b
B	c	d

Variability in strategy in the population

Payoffs

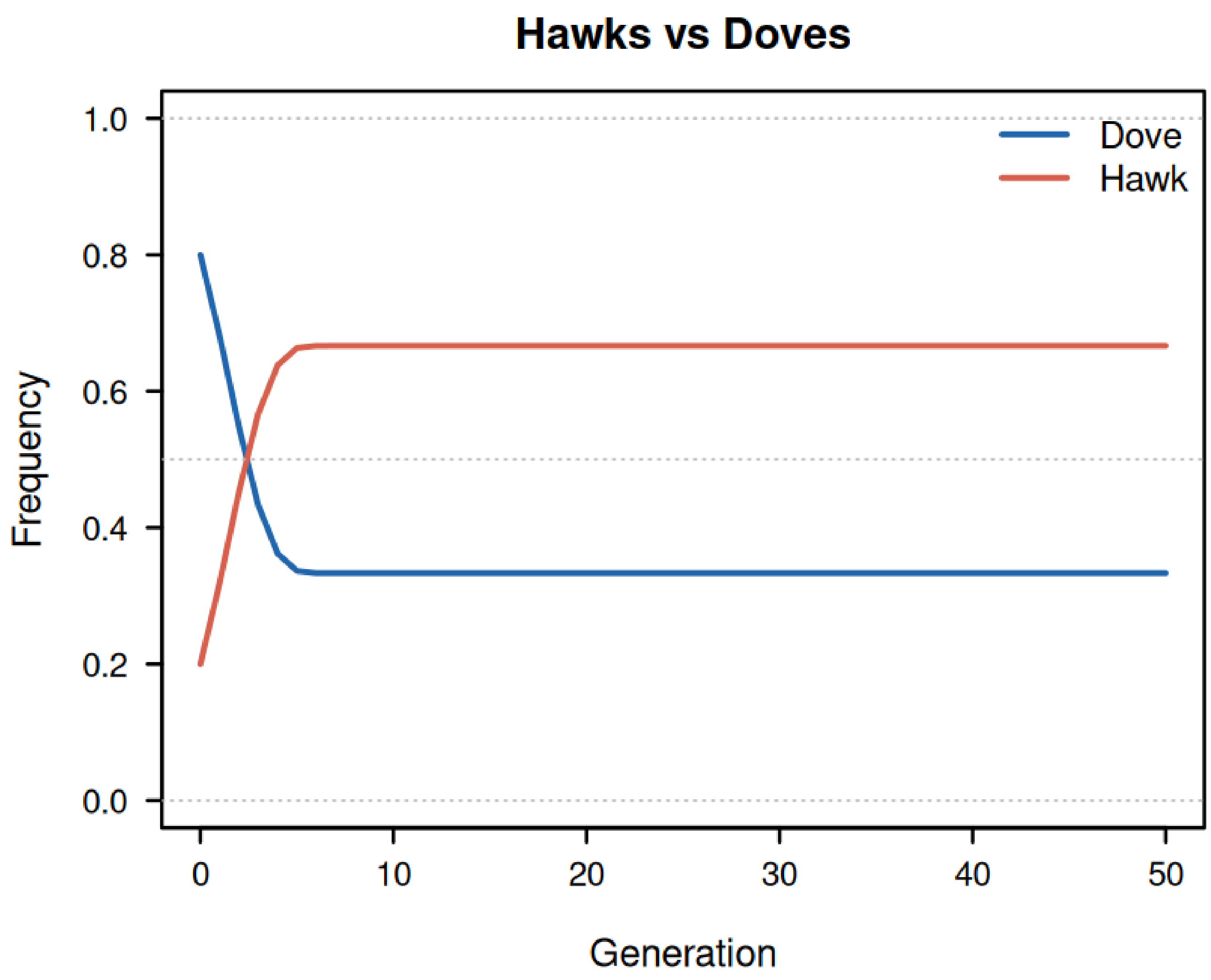
$$\dot{x} = x(1-x)[(a-b-c+d)x+b-d].$$

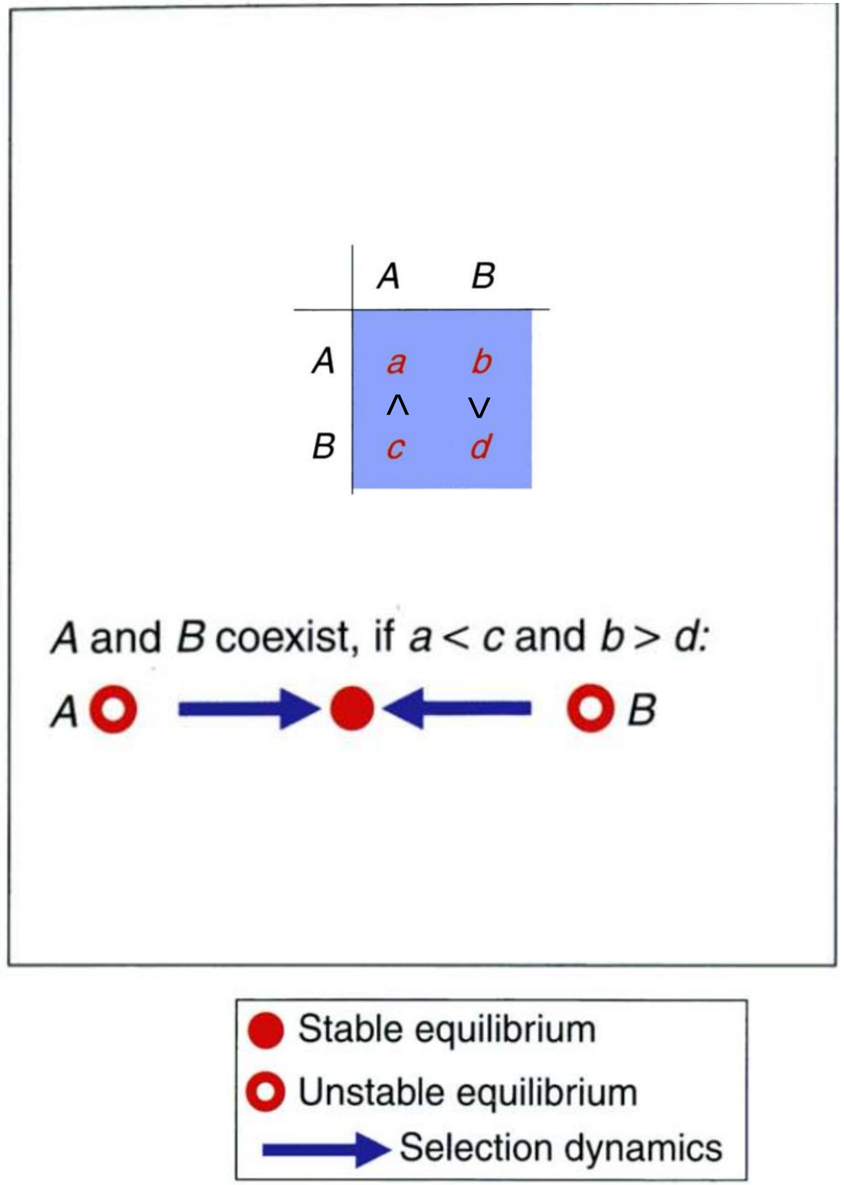
Replicator's equation



Evolutionary dynamics: hawks and doves

	Hawk	Dove
Hawk	-1,-1	4,0
Dove	0,4	2,2





Evolutionary dynamics: hawks and doves

	Hawk	Dove
Hawk	-1,-1	4,0
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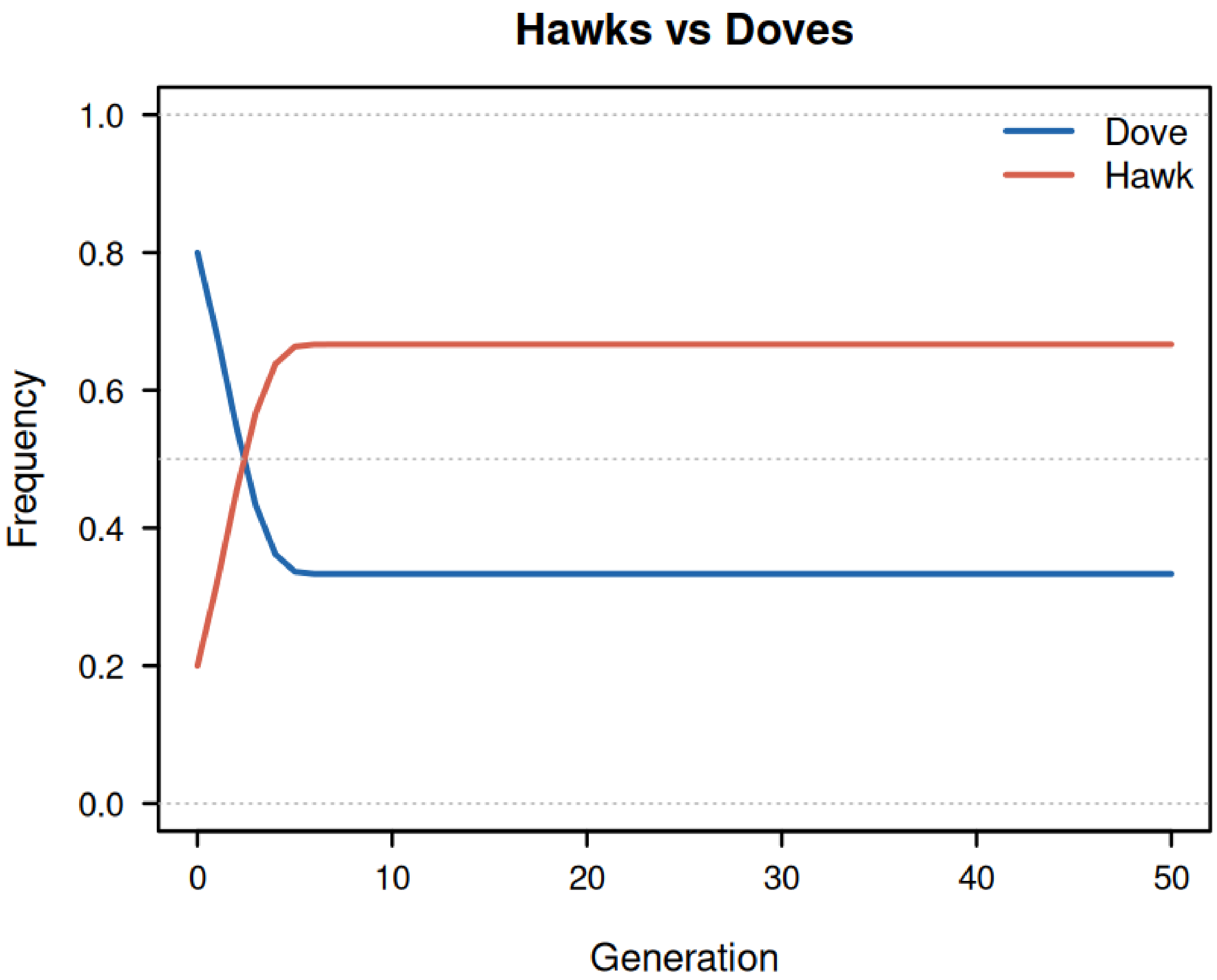
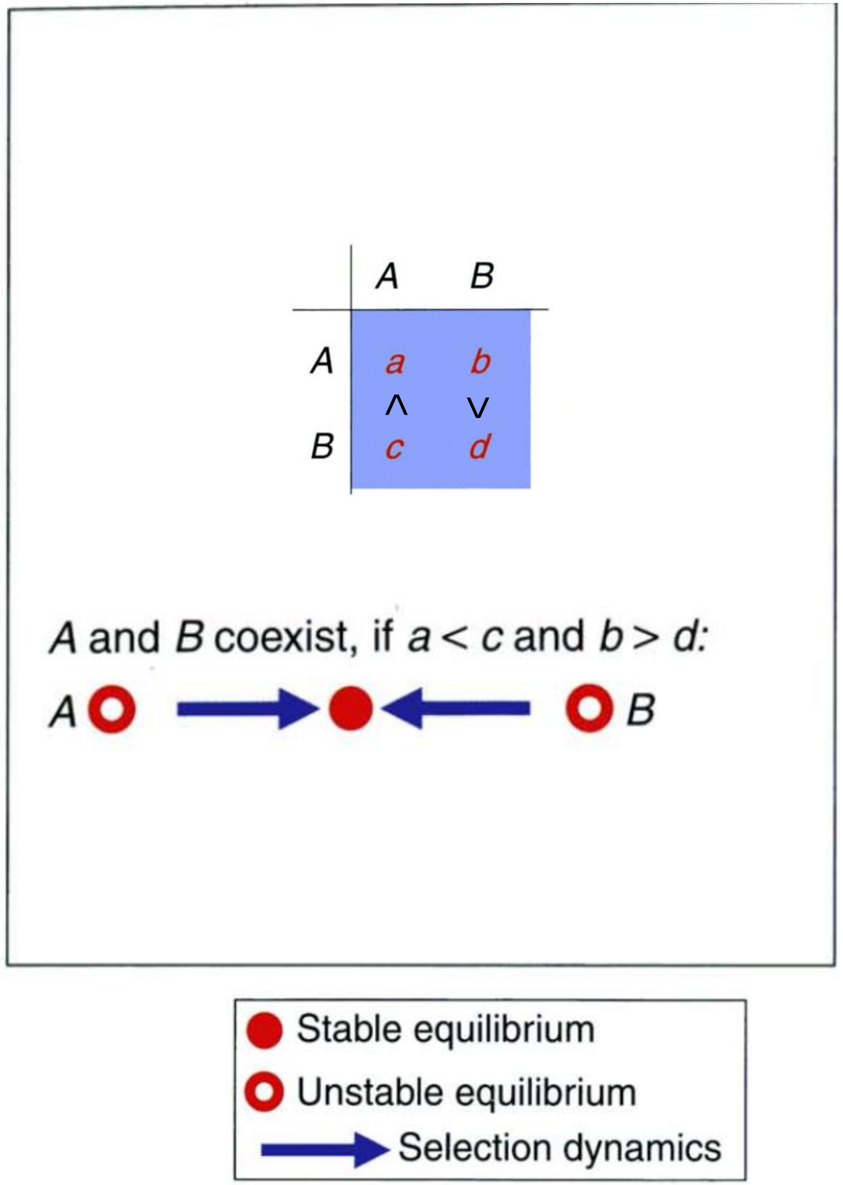


Unstable equilibrium 100% Hawks

Stable equilibrium (ESS) 2/3 Hawks

Unstable equilibrium 0% Hawks



Evolutionary dynamics: Batesian mimicry

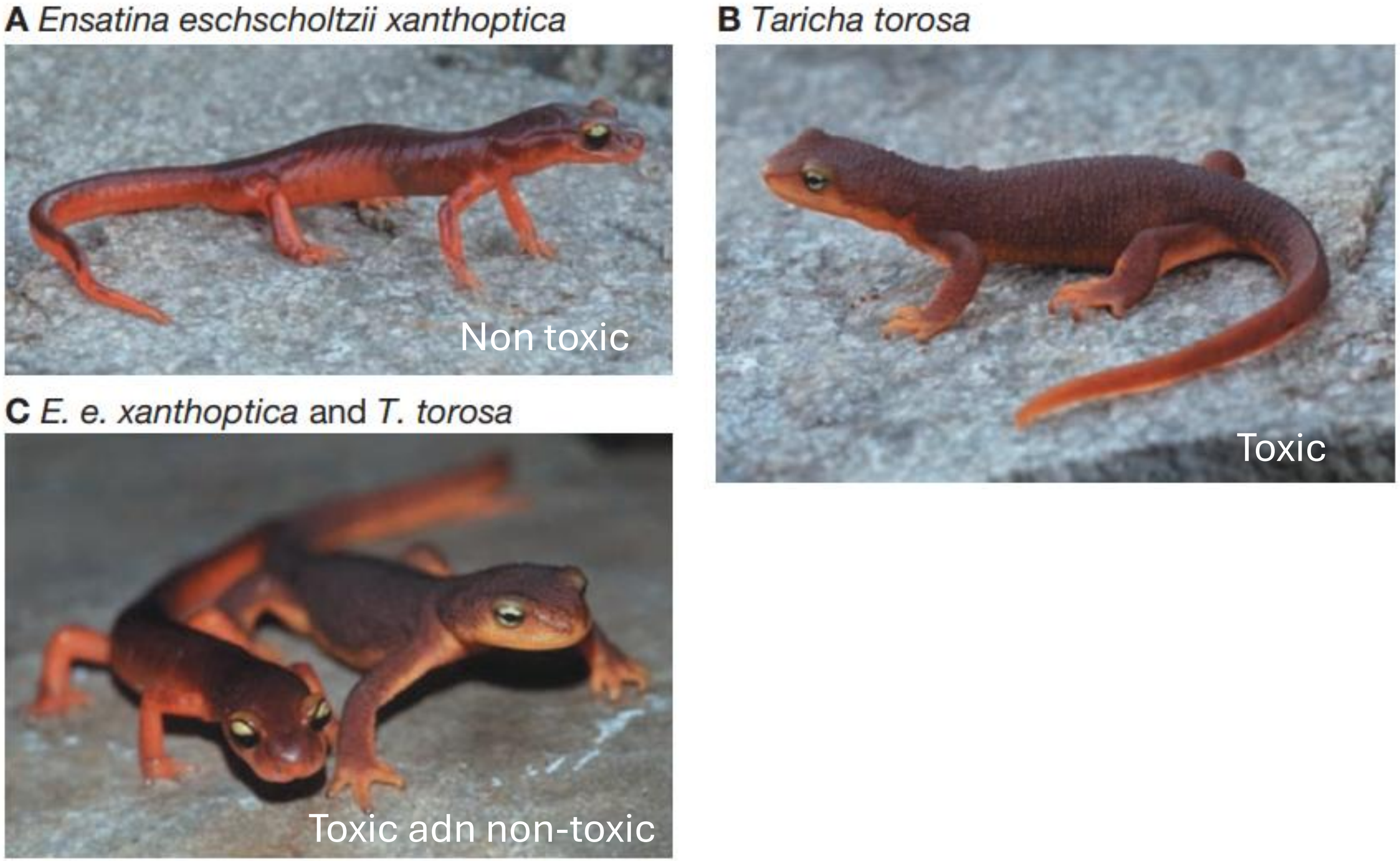


FIGURE 18.16 Mimicry and coevolution. **(A)** The nontoxic mimic, *Ensatina eschscholtzii xanthoptica*, **(B)** the toxic model, *Taricha torosa*, **(C)** the mimic (*E. e. xanthoptica*, on the left) and the toxic model (*T. torosa*, on the right) together

Evolutionary dynamics: Batesian mimicry

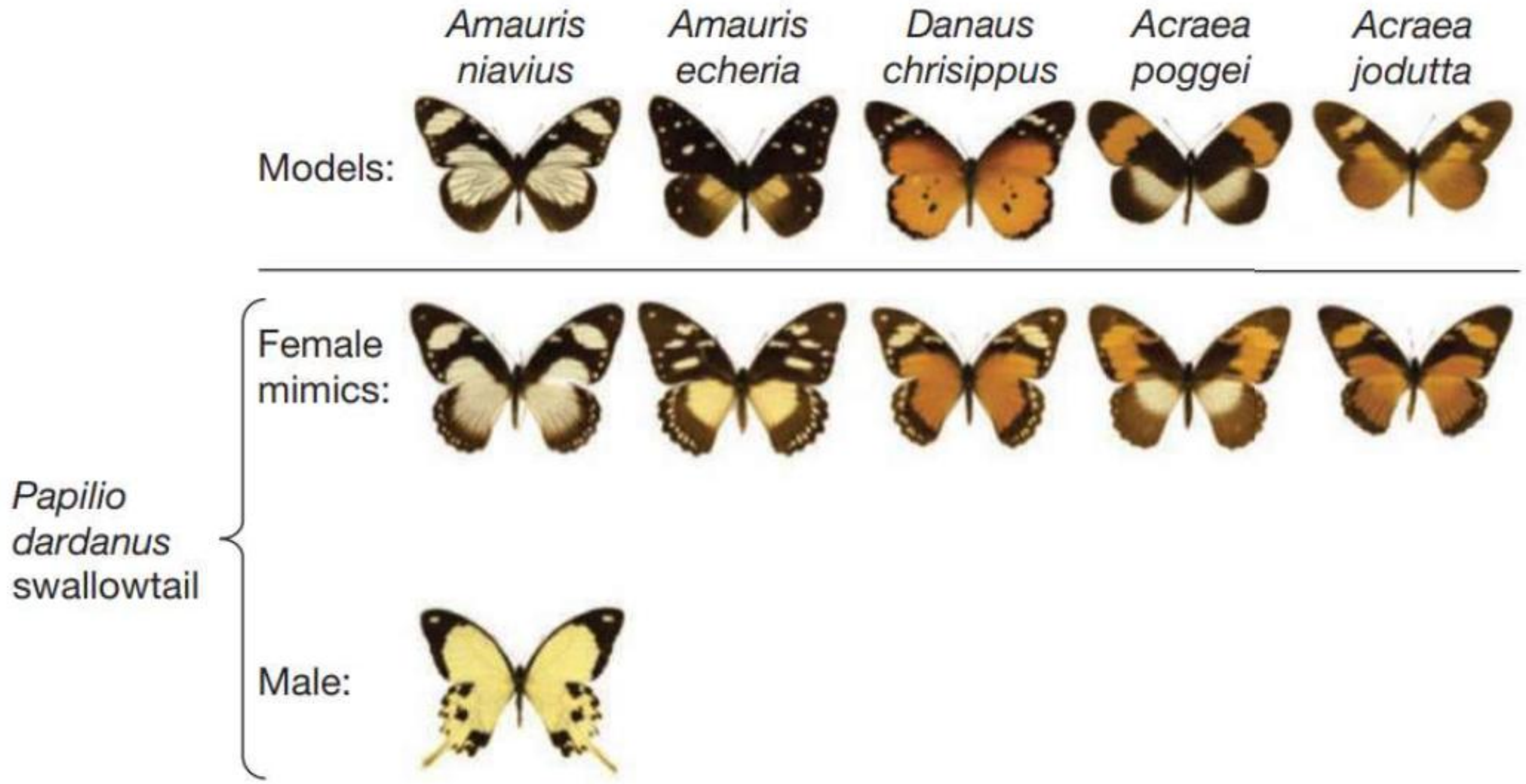


FIGURE 13.10 Mimetic polymorphism in the African swallowtail butterfly *Papilio dardanus*. Males have only one color form (at bottom), but populations contain several color forms of females (mimics, in the middle row), each of which closely resembles a distantly related distasteful species (models, in the top row). Predators that have attacked a distasteful model learn to avoid butterflies with that color pattern. As the abundance of any specific color morph of *P. dardanus* increases, its fitness tends to decline, because predators are increasingly likely to associate the pattern with a tasty meal rather than a foul taste. (From [75].)

Evolutionary dynamics: Batesian mimicry

Model vs Model (0.85)	1 − s	Genuine defence works, but toxin production costs 15% fitness
Model vs Mimic (0.75)	1 − s − δ	Toxin cost plus signal dilution by mimics eroding predator avoidance
Mimic vs Model (1.00)	full survival	Mimic free-rides on reliable signal, no toxin cost — maximum fitness
Mimic vs Mimic (0.40)	1 − c	Signal so diluted predators attack freely — heavy survival penalty

Amauris niavius

Amauris niavius

	Model	Mimic
Model	0.85, 0.85	0.75, 1
Mimic	1, 0.75	0.4, 0.4

Evolutionary dynamics: Batesian mimicry

Model vs Model (0.85)	1 – s	Genuine defence works, but toxin production costs fitness (s=15%)
Model vs Mimic (0.75)	1 – s – d	Toxin cost plus signal dilution by mimics eroding predator avoidance (d=10%)
Mimic vs Model (1.00)	full survival	Mimic free-rides on reliable signal, no toxin cost — maximum fitness
Mimic vs Mimic (0.40)	1 – c	Signal so diluted that predators attack freely (c=60%)

Amauris niavius

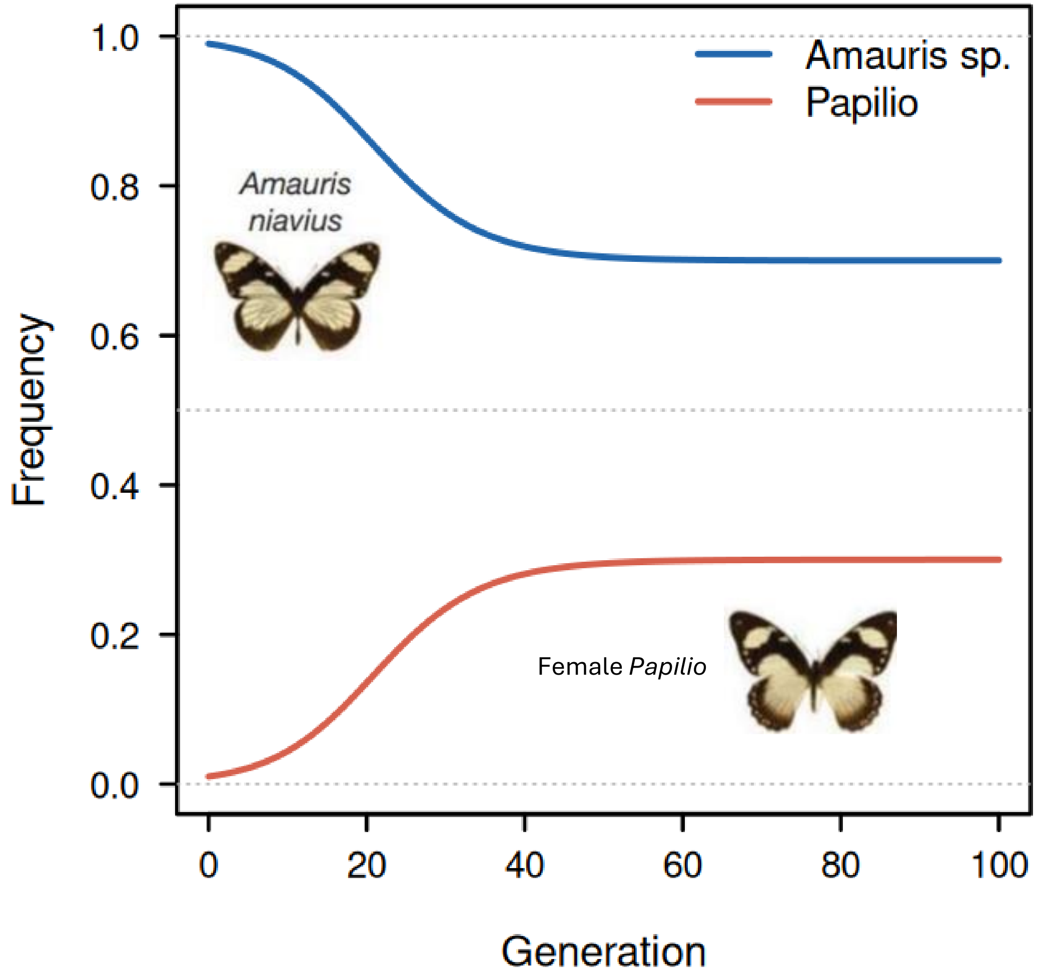
Female *Papilio*

Amauris niavius

Female *Papilio*

	Model	Mimic
Model	0.85, 0.85	0.75, 1
Mimic	1, 0.75	0.4, 0.4

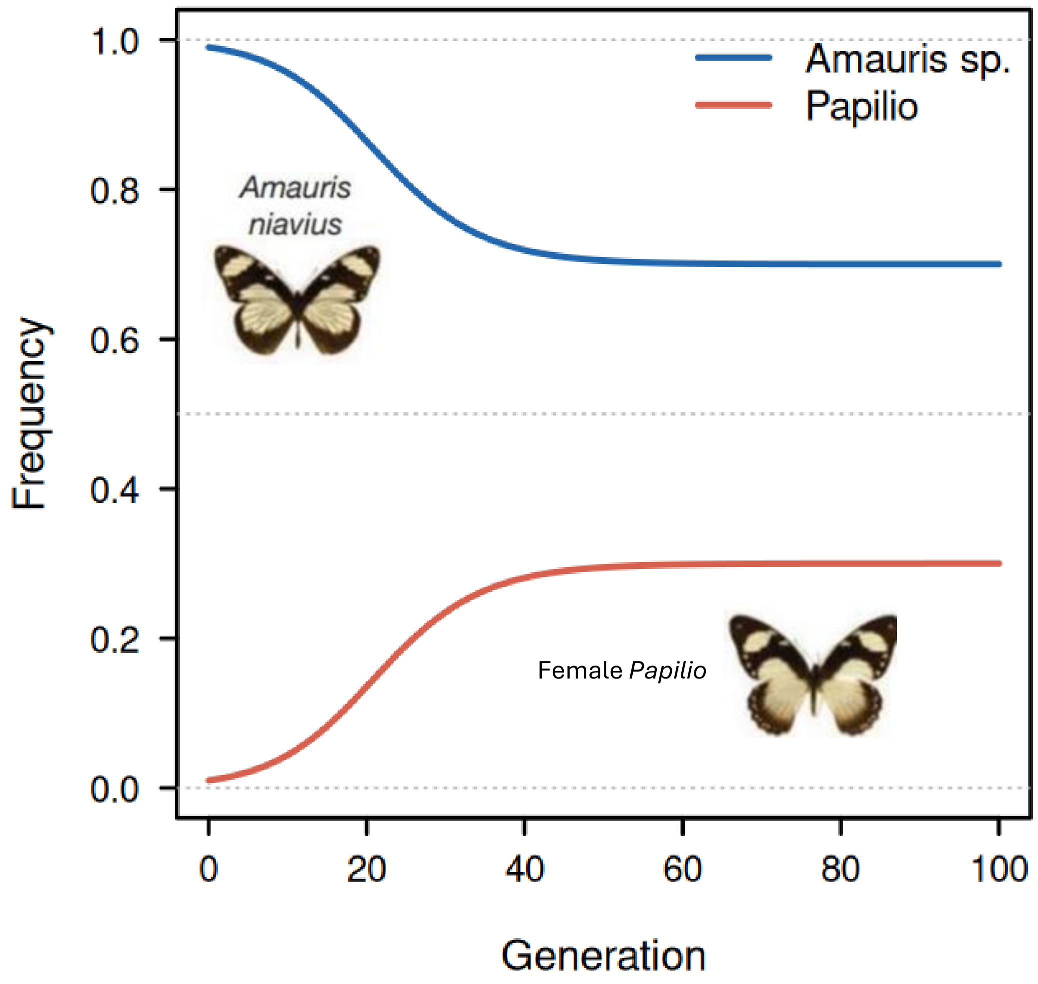
Evolutionary dynamics: Batesian mimicry



What happens?

	Model	**Mimic**
Model	0.85, 0.85	0.75, 1
Mimic	1, 0.75	0.4, 0.4

Evolutionary dynamics: Batesian mimicry



Unstable equilibrium 100% models

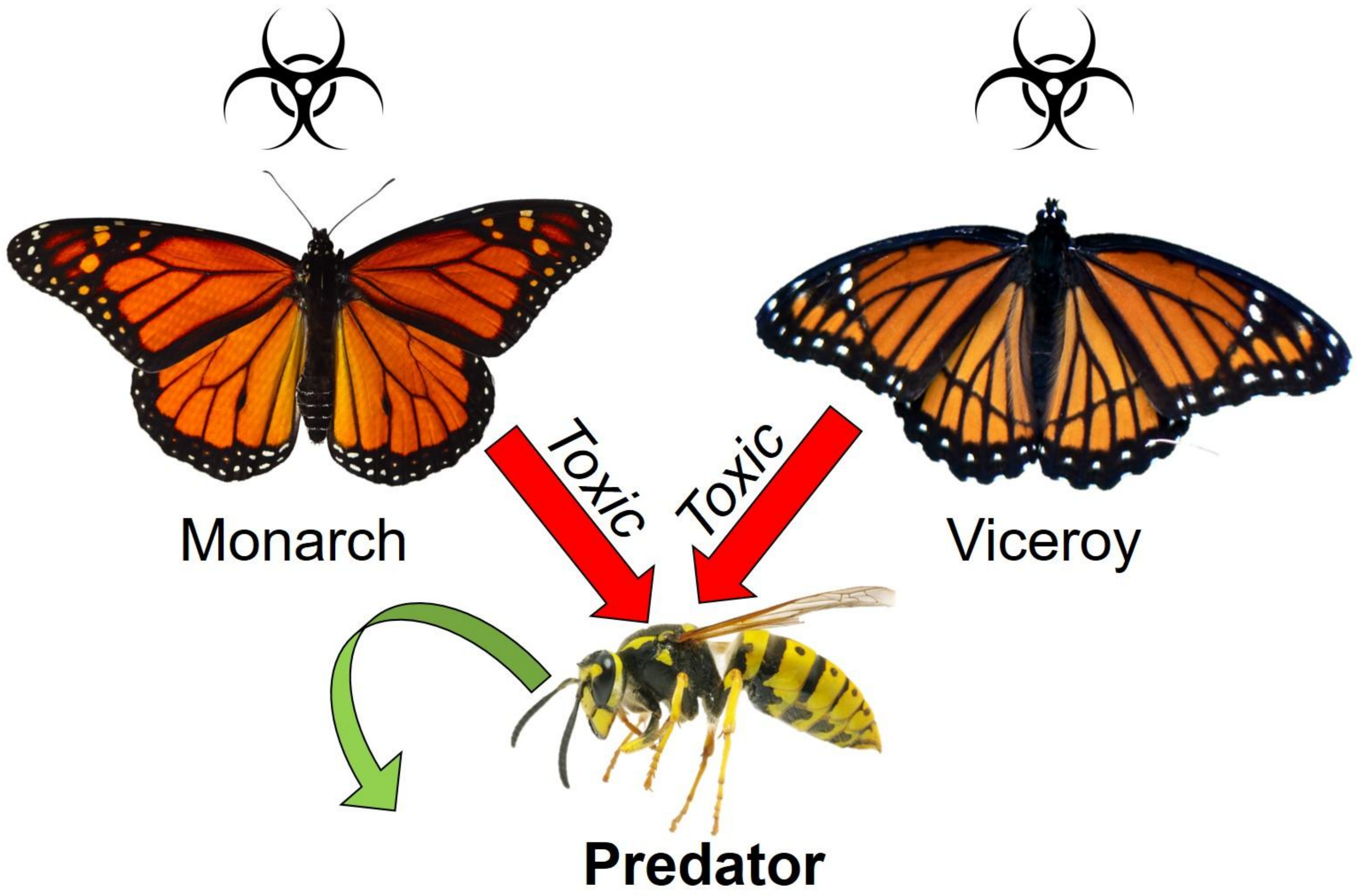
Stable equilibrium (ESS)

Unstable equilibrium 0% Mimics

What happens?
Mimics can invade but it cannot spread to much since birds stops avoiding eating butterflies, leading to «Hawk and Dove» dynamics

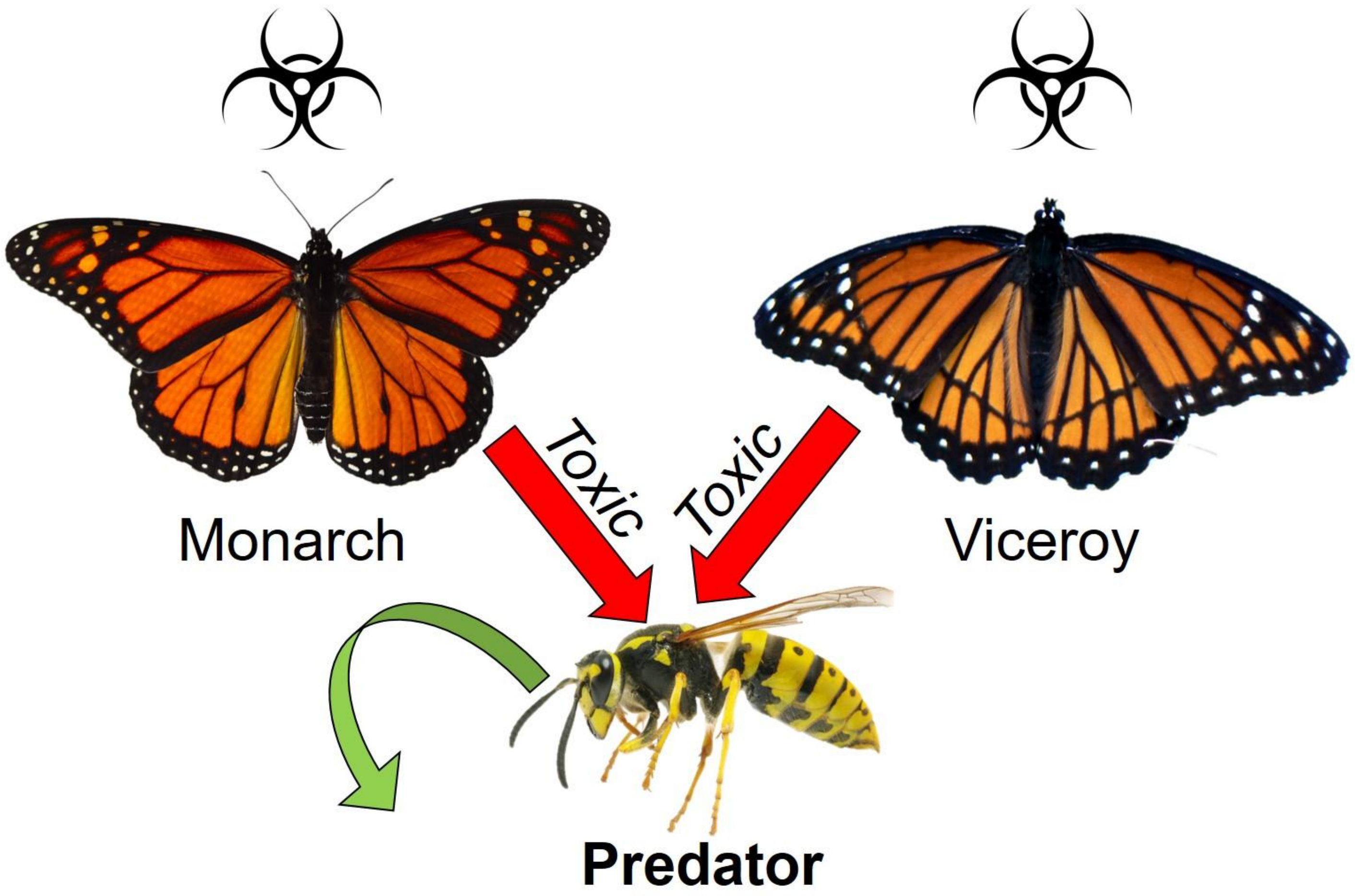
	Model	**Mimic**
Model	0.85, 0.85	0.75, 1
Mimic	1, 0.75	0.4, 0.4

Müllerian mimicry



- *A (somewhat familiar) example of Müllerian mimicry with two species of butterflies, the **monarch** and the **viceroy**. Although this has traditionally been thought of as a textbook case of Batesian mimicry (see below), the **toxicity of both species** likely makes it a scenario of Müllerian mimicry instead. Since both butterflies **share the same pattern and both are toxic**, it sends a strong signal to predators such as wasps to avoid them both.*

Müllerian mimicry: what game would it be?



- *A (somewhat familiar) example of Müllerian mimicry with two species of butterflies, the **monarch** and the **viceroy**. Although this has traditionally been thought of as a textbook case of Batesian mimicry (see below), the **toxicity of both species** likely makes it a scenario of Müllerian mimicry instead. Since both butterflies **share the same pattern and both are toxic**, it sends a strong signal to predators such as wasps to avoid them both.*

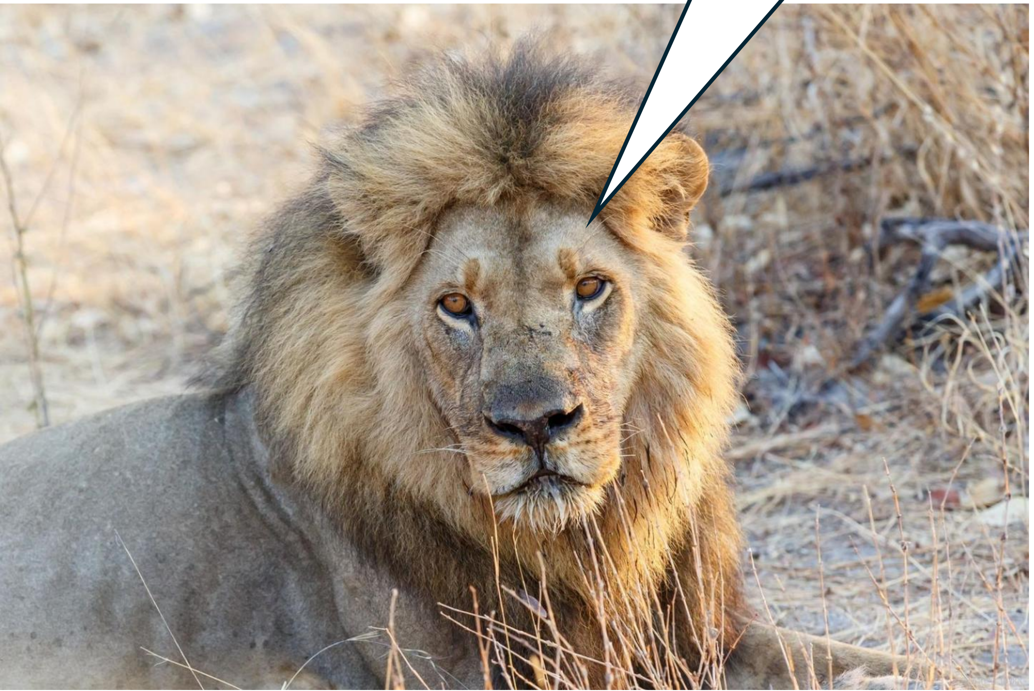

trick J. Endres / AlaskaPhotoGraphics.com

Coordination games/stag hunt

	Cooperation (stag/buffalo)	**Defection (hare)**
Cooperation (stag/buffalo)	1, 1	0, 0.3
Defection (hare)	0.3 , 0	0.3, 0.3

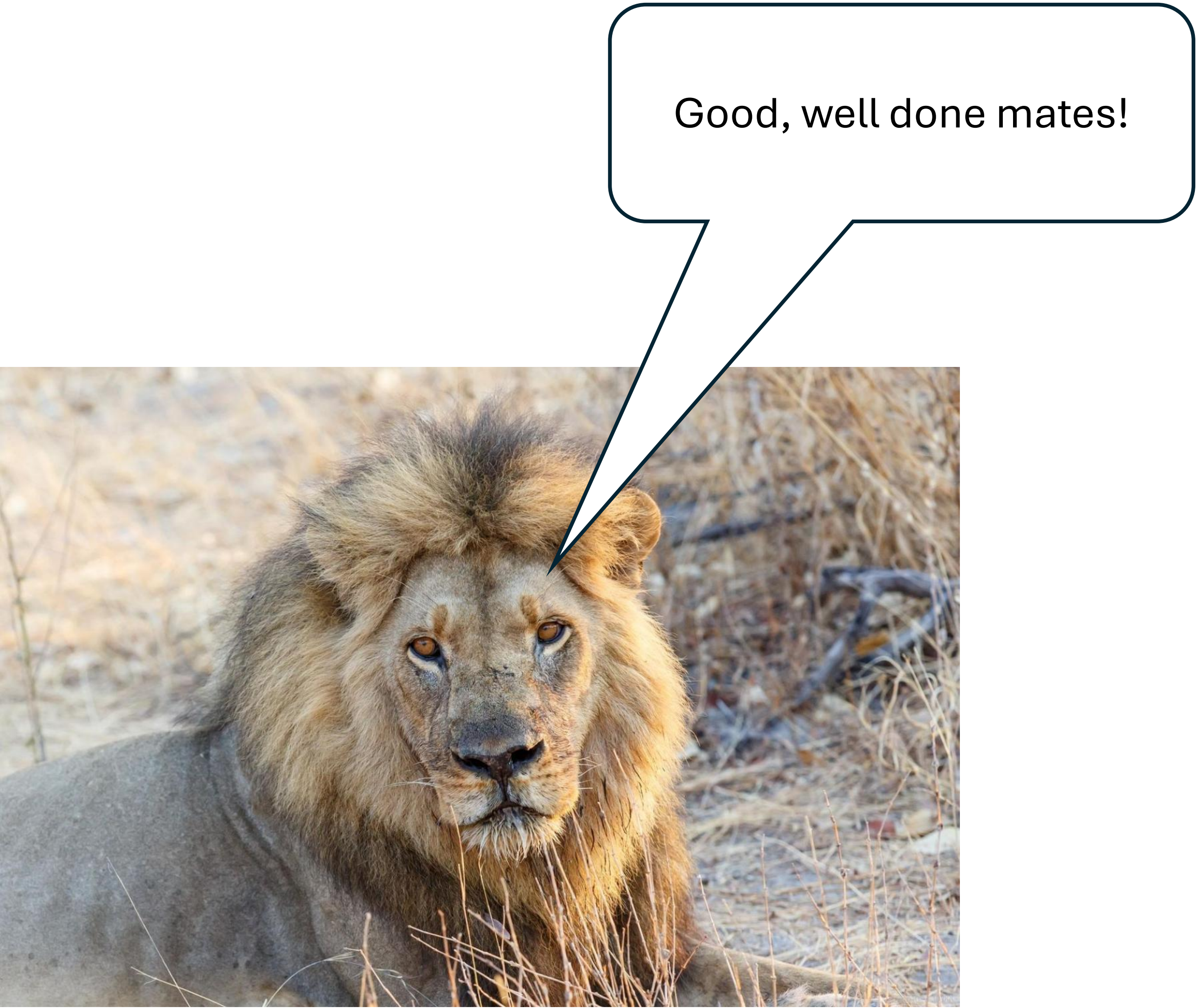
Coordination games/stag hunt

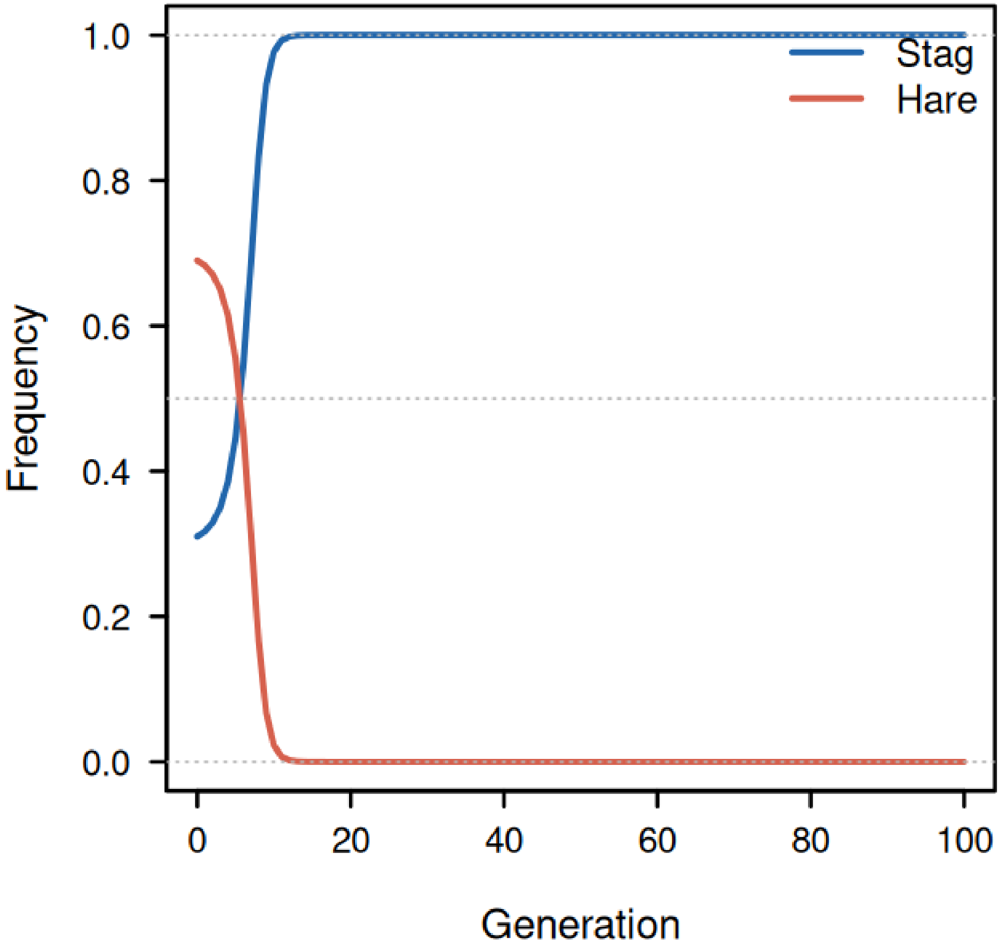
What happens? ROAARR



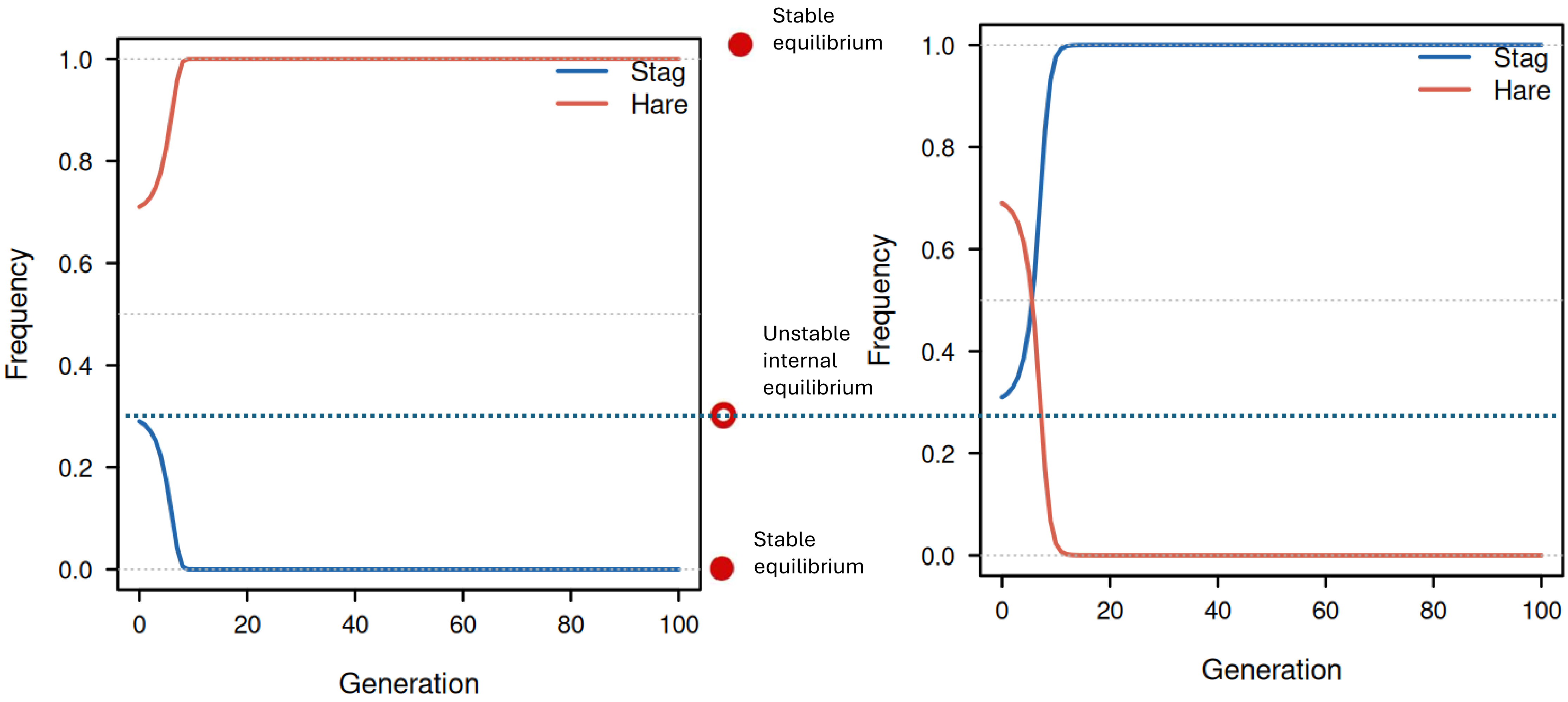
	Cooperation (stag/buffalo)	Defection (hare)
Cooperation (stag/buffalo)	1, 1	0, 0.3
Defection (hare)	0.3 , 0	0.3, 0.3

Coordination games/stag hunt





Coordination games/stag hunt



The general structure of 2-players' games

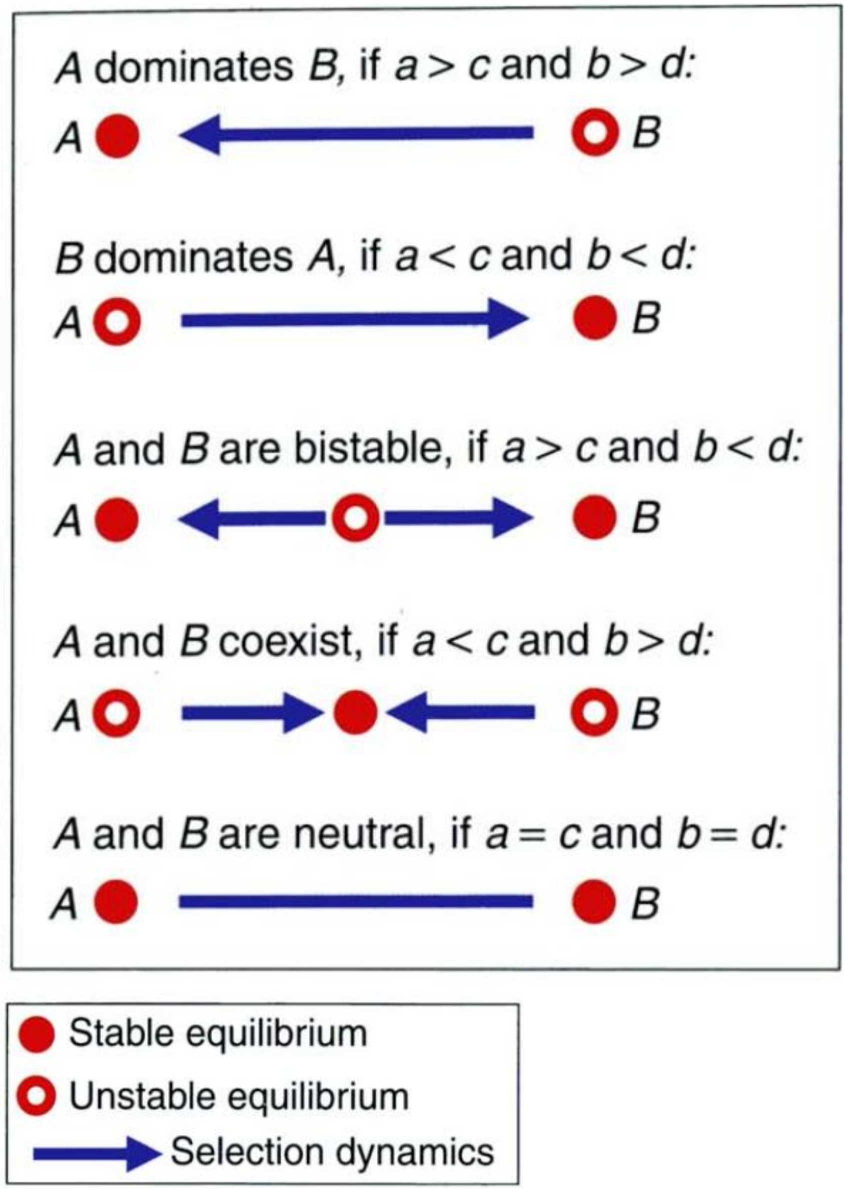
	A	B
A	a	b
B	c	d

Variability in strategy in the population

Payoffs

$$\dot{x} = x(1-x)[(a-b-c+d)x + b - d].$$

Replicator's equation



Coordination games/stag hunt

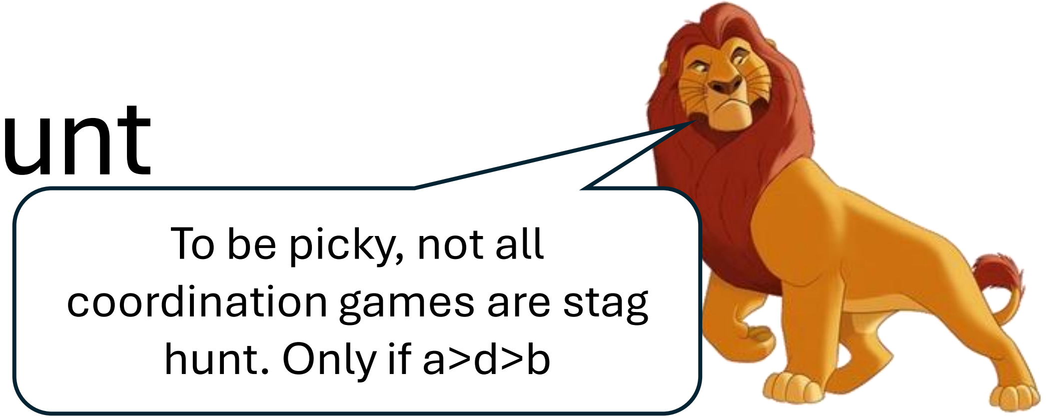
•**Large prey** (buffalo, giraffe, zebra) — requires coordination, higher payoff per individual if successful, but risky and likely to fail if others don't cooperate
•**Small prey** (hares, small antelopes) — catchable alone, lower payoff but safe

Lionesses do most of the hunting, and within a pride they tend to adopt **consistent roles** — some are "centers" that chase prey toward others, some are "wings" that flank. This role specialization suggests repeated coordination over time, which is exactly how the cooperative equilibrium gets stabilized in iterated versions of the stag hunt.

However classic work by **Packer & Ruttan (1988)** and later **Heinsohn & Packer (1995)** showed that some individuals consistently **free-ride** — they lag behind during the hunt but share the kill.

This suggests the game lions are playing may be closer to a **prisoner's dilemma** than a pure stag hunt in some contexts.

Coordination games/stag hunt



	A	B
A	a	b
B	c	d

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Red queen dynamics
“It takes all the running you can do, to keep in the same place.”

The **Red Queen** comes from *Through the Looking-Glass* (1871) by Lewis Carroll.

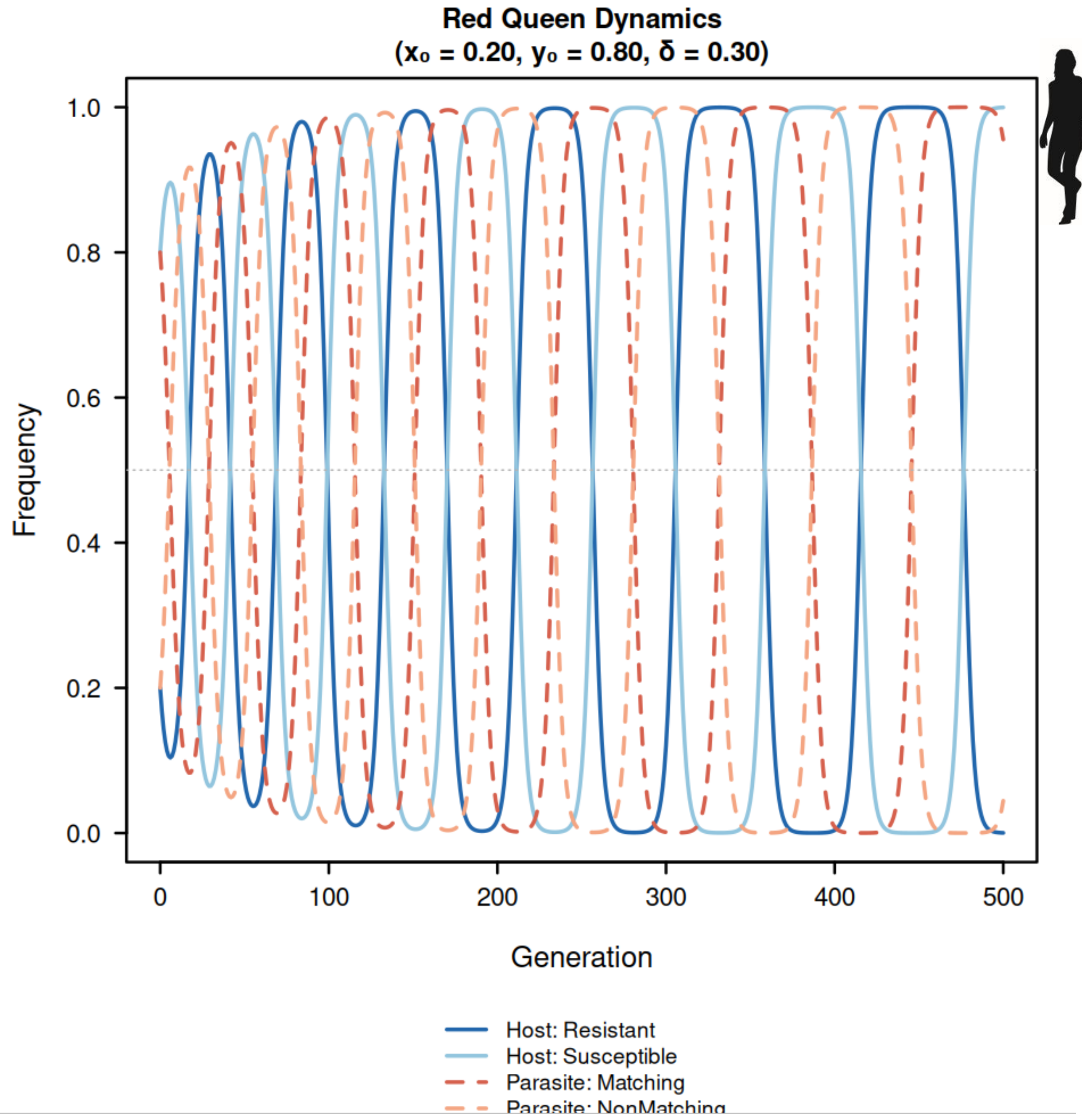
The **Red Queen hypothesis** (coined by Leigh Van Valen) means:

- Species must **constantly evolve**
- Just to **maintain their relative fitness**
- Because:
  - competitors evolve
  - parasites evolve
  - environments change
- Evolution as a **continuous arms race**

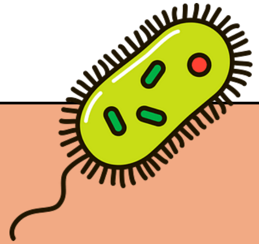
Classic examples

- Host ↔ parasite coevolution
- Predator ↔ prey
- Immune system ↔ pathogens

Red queen dynamics

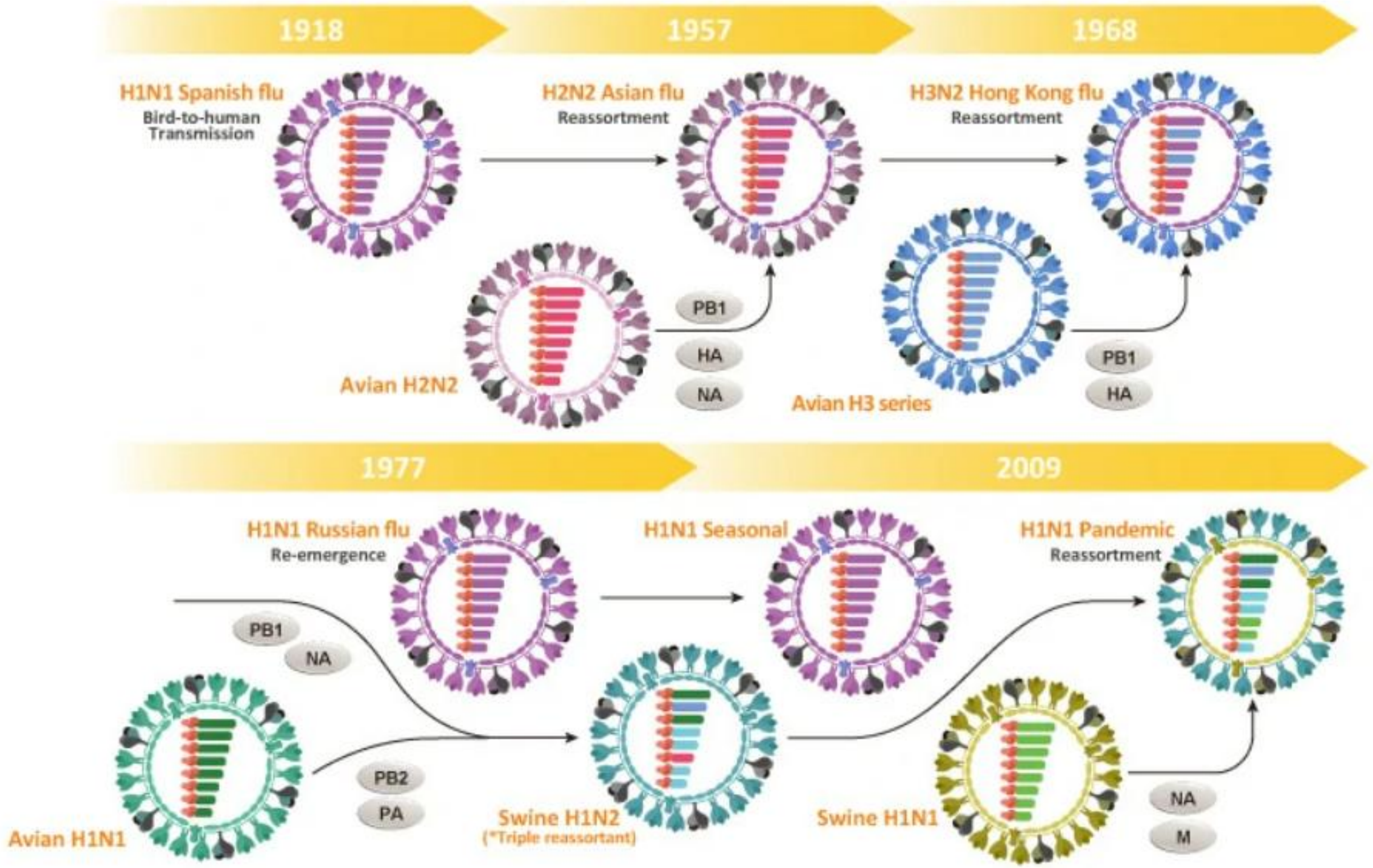


	Matching	Non Matching
Resistant	1	0
Susceptible	0	1



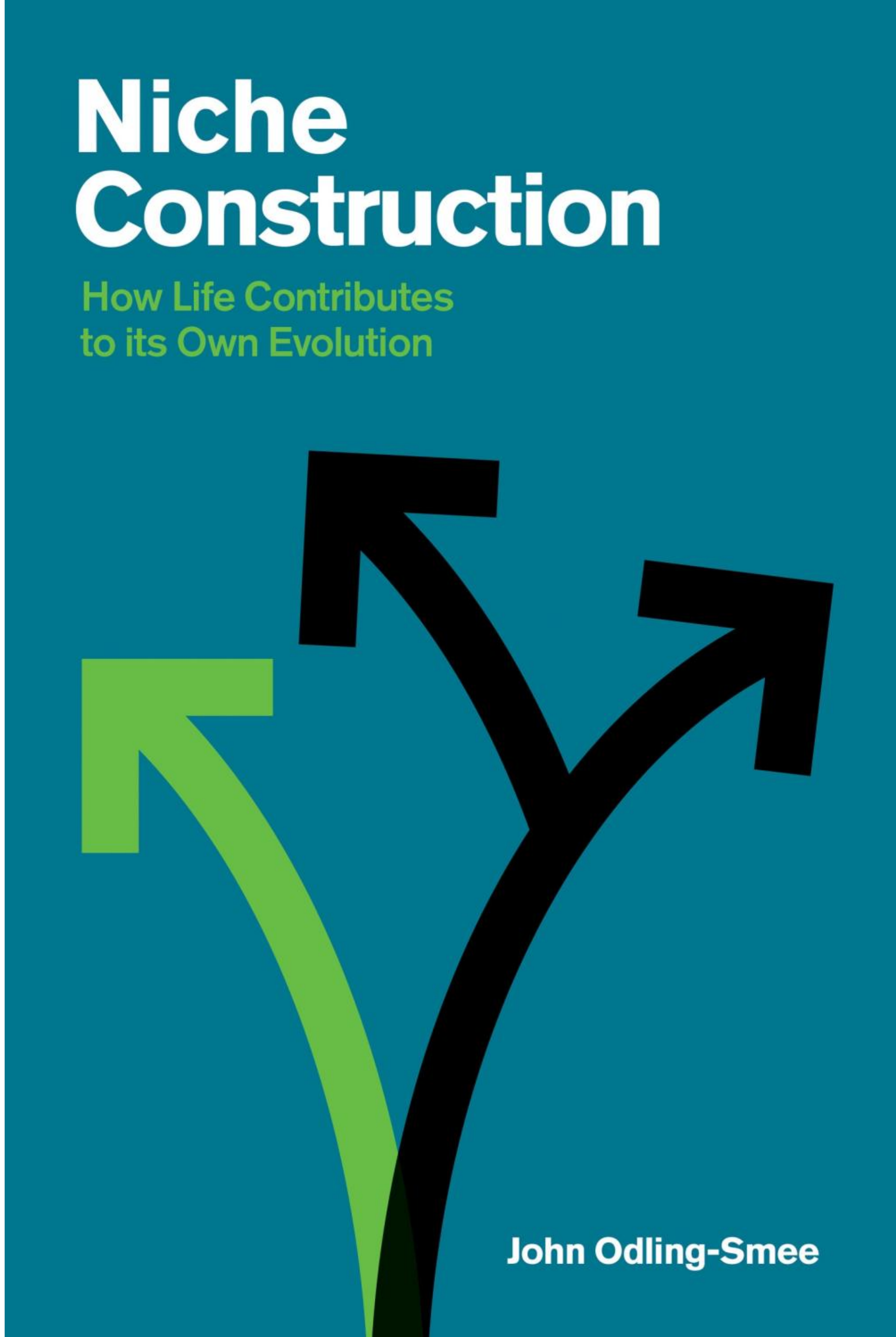
	Resistant	Susceptible
Matching	1	0
Non Matching	0	1

The influenza virus displays typical Red Queen dynamics



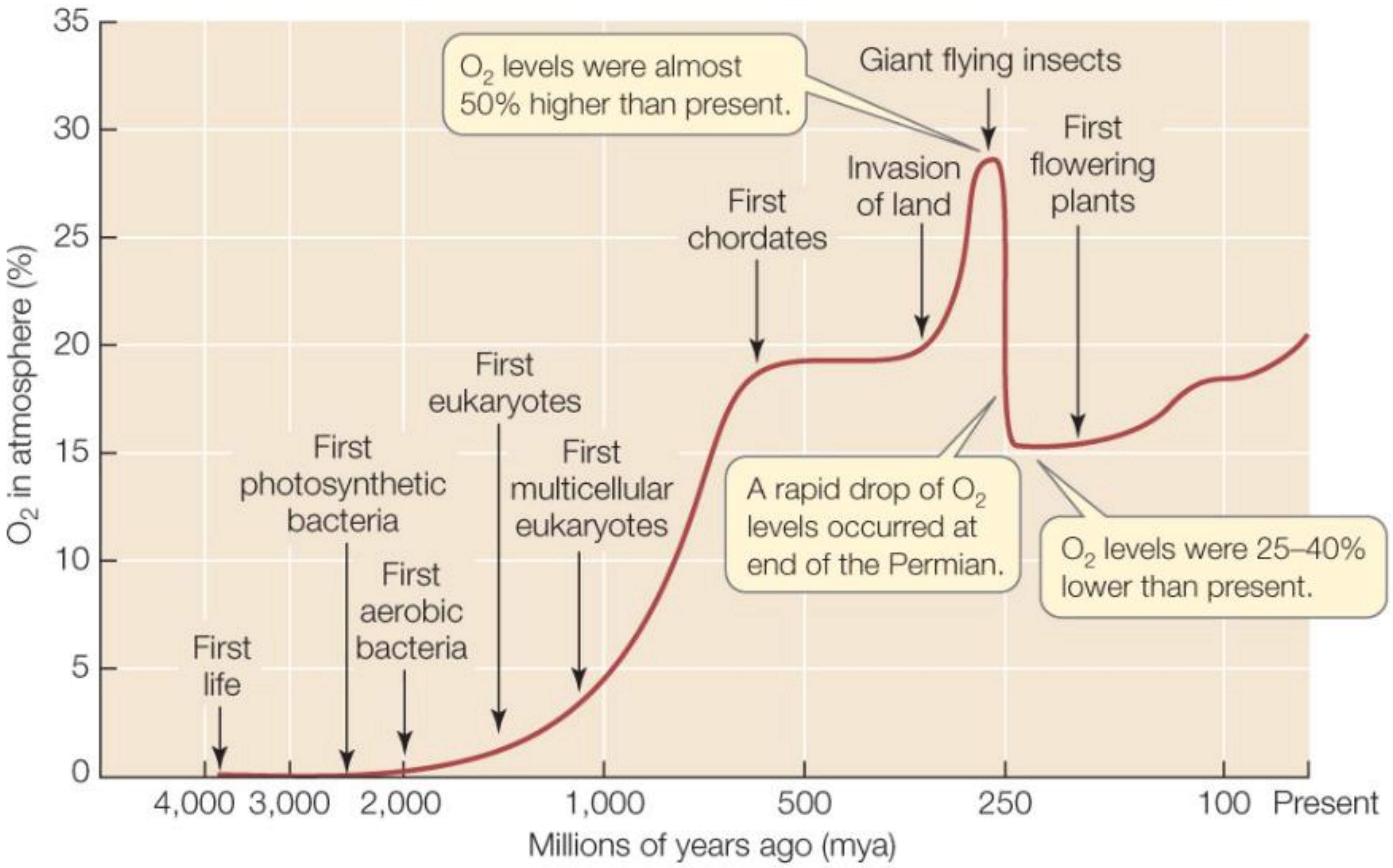
Niche construction

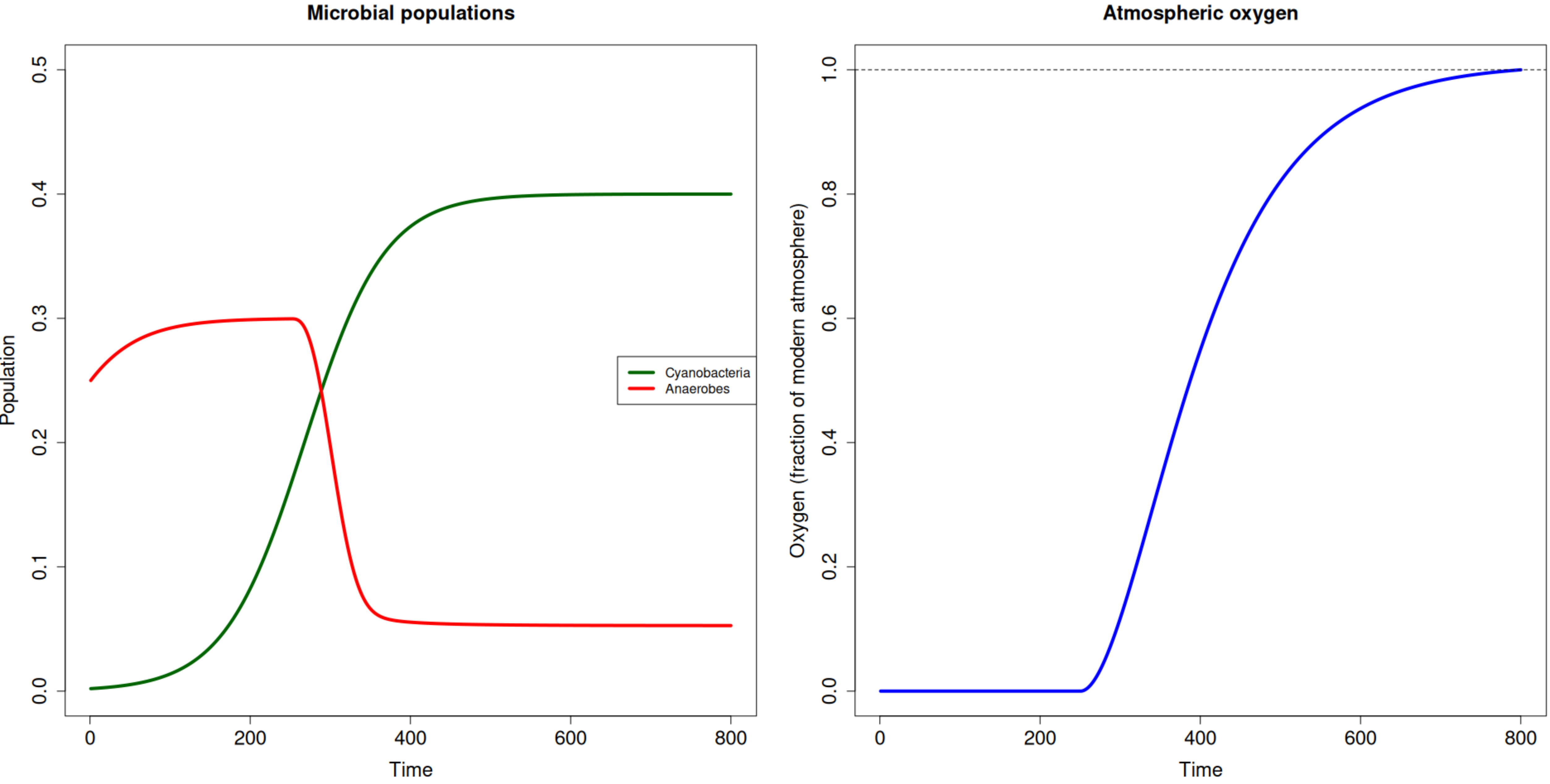
- Organisms **actively modify their environment**
- These modifications **change selection pressures**
- Evolution is not just:
    - environment → organism
      but also:
    - **organism → environment → organism**
- Feedback loop between ecology and evolution
- **Standard vs Niche Construction View**
- **Standard view**
    - Environment is **external and fixed**
    - Selection acts on organisms
- **Niche construction**
    - Environment is **partly constructed by organisms**
    - Organisms **co-direct their own evolution**




THE GREAT OXYGENATION EVENT
THE AIR WE BREATHE

The great oxygenation event





Microbial populations
Population
Time
Cyanobacteria
Anaerobes
0.0
0.1
0.2
0.3
0.4
0.5
0
200
400
600
800
Atmospheric oxygen
Oxygen (fraction of modern atmosphere)
Time
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800