

# COEVOLUTION



## ¿Qué es coevolución?

Coevolución es aquel proceso por el cual dos o más organismos ejercen presión de selección mutua y sincrónica (en tiempo geológico) que resulta en adaptaciones específicas recíproca.

Janzen 1980

### Requisitos del proceso de coevolución

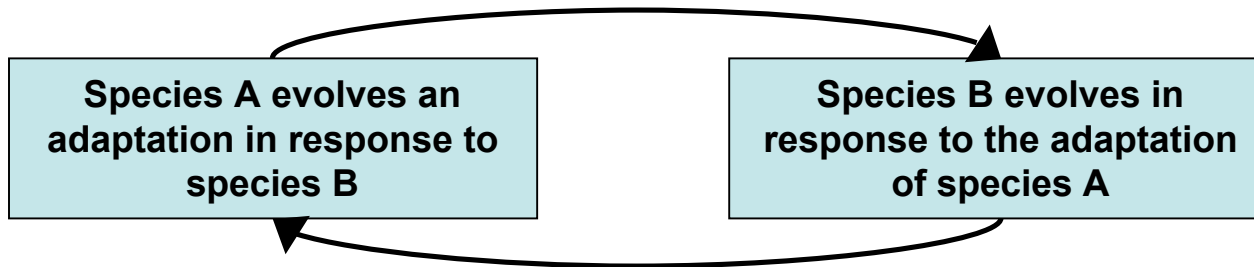
- 1) **Especificidad:** la evolución de cada rasgo en una especie es debida a presiones selectivas de otros rasgos de las otras especies del sistema.
- 2) **Reciprocidad:** los rasgos en ambos participantes del sistema evolucionan conjuntamente.
- 3) **Simultaneidad:** los rasgos en ambos participantes del sistema evolucionan al mismo tiempo.

$$R_1 = h_1^2 S_1(\phi_2)$$

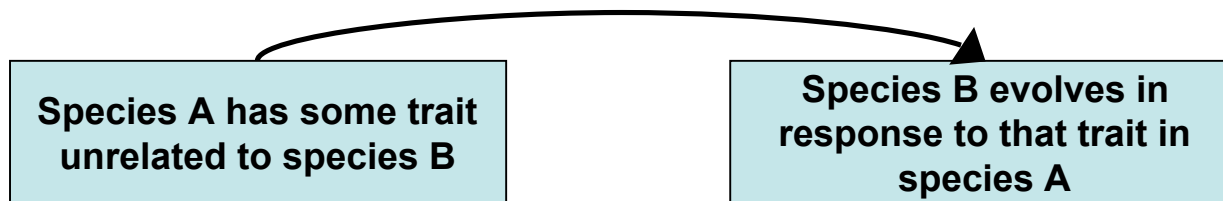
$$R_2 = h_2^2 S_2(\phi_1)$$

$\phi_i$  is the genotypic distribution of species i

What it is coevolution



What it isn't coevolution



El proceso coevolutivo puede generar

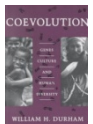
- 1) Coadaptación: ajuste microevolutivo recíprocos de unos organismos a otros (**Micro-coevolución**).
- 2) Coespeciación: cladogénesis recíproca como fruto de la interacción (**Macro-coevolution**).

## **MicroCoevolution**

The outcome of the coevolutionary process largely depends on:

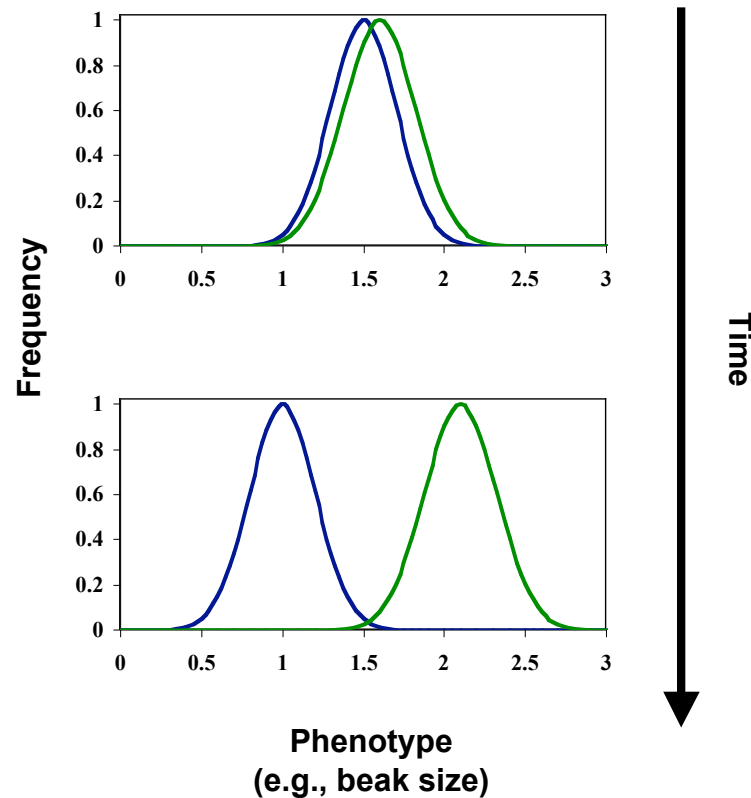
1. The type of ecological interaction. The interactions differ in the form of reciprocal selection
2. The genetic mediation of the interaction

- Competitive interactions lead to divergence
- Antagonistic interactions lead to cycles or escalation
- Mutualistic interactions lead to convergence



## MicroCoevolution

### Coevolution in competitive interactions



#### Reciprocal Selection:

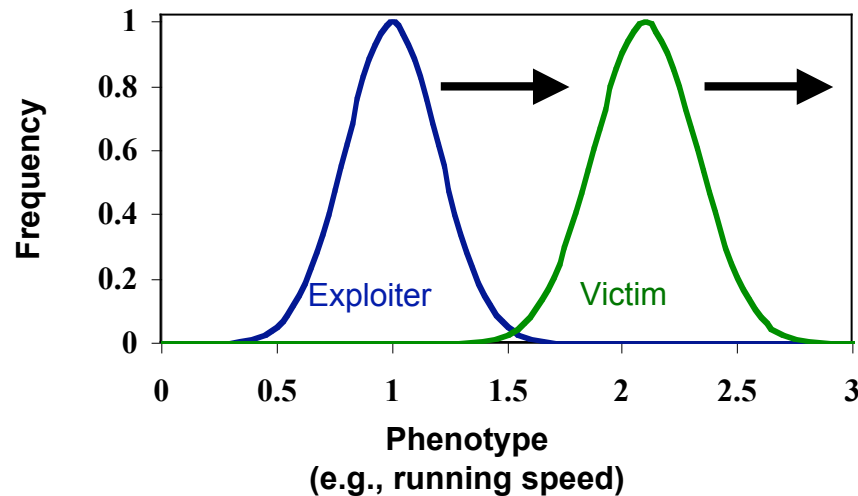
- The fitness of Species 1 individuals is decreased by interacting with Species 2
- The fitness of Species 2 individuals is decreased by interacting with Species 1
- Reciprocal selection favors traits in each species that reduce the efficacy or frequency of the interaction

#### Coevolutionary dynamics:

- Divergence in traits mediating the interaction (i.e., character displacement)

## MicroCoevolution

### Coevolution in antagonistic interactions



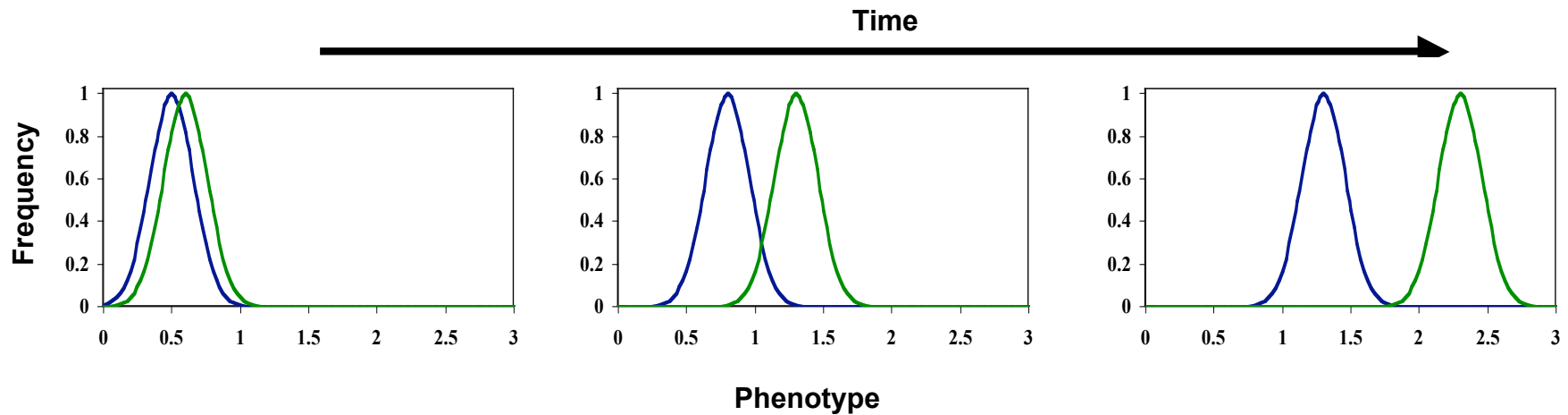
#### Reciprocal Selection:

- The fitness of victim individuals is increased by not interacting
- The fitness of exploiter individuals is increased by interacting
- Reciprocal selection favors victim traits that decrease the efficacy or frequency of interaction, but exploiter traits that increase the efficacy or frequency of the interaction

- **Coevolutionary escalation** – Reciprocal selection favors increased (or decreased) phenotypes in both victim and exploiter. Selection is directional
- **Coevolutionary matching** – Reciprocal selection favors exploiters that match the phenotype of the victim, but victims that mismatch the phenotype of the exploiter. Selection is time-delayed negative frequency-dependent

**MicroCoevolution**

**Coevolution in antagonistic interactions: Coevolutionary escalation**

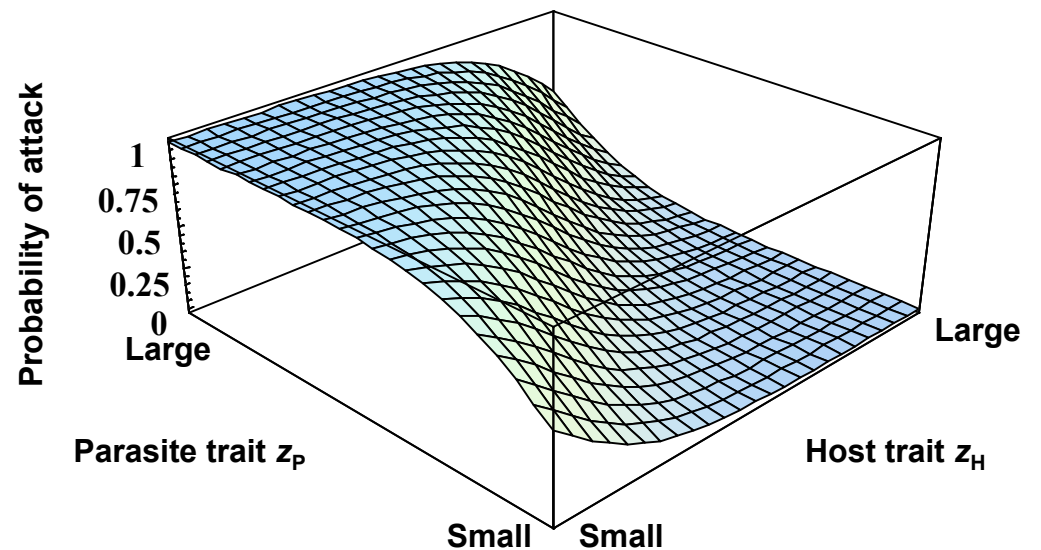


**Coevolutionary dynamics:**

- Without cost: Endless escalation of phenotypes
- With cost: Phenotypic cycles

**Examples:**

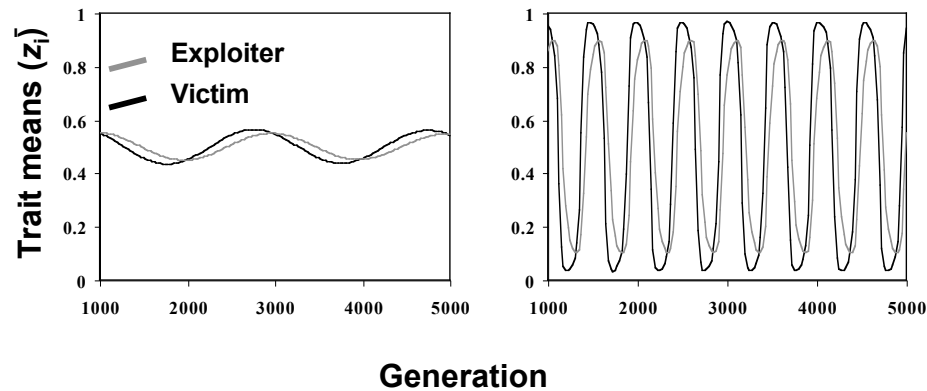
- Concentration of plant defensive compounds
- Concentration of insect detoxification enzymes





**MicroCoevolution**

**Coevolution in antagonistic interactions: Coevolutionary matching**

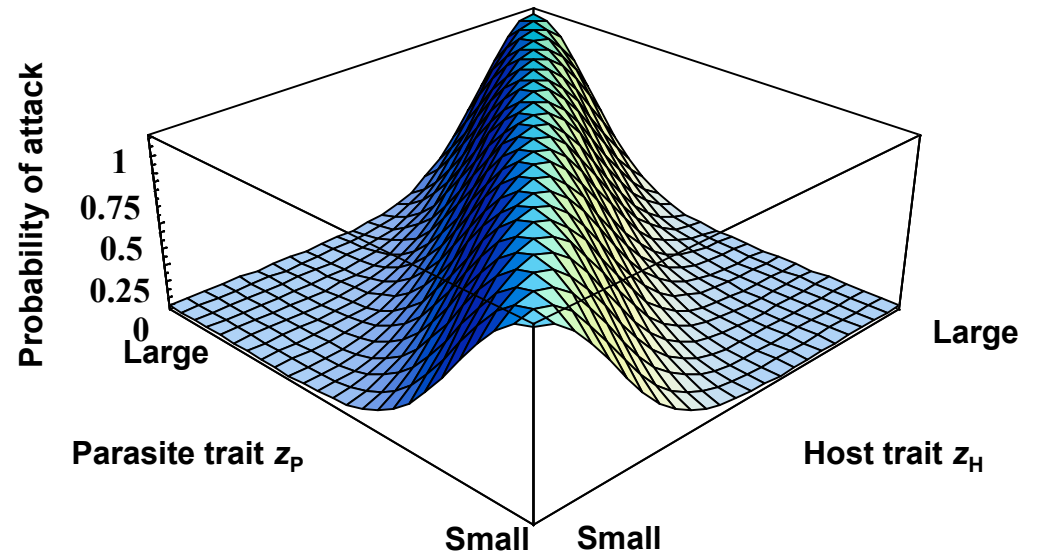


**Coevolutionary dynamics:**

- Phenotypes cycle endlessly
- Exploiter adapts to common victim phenotypes
- Should produce an advantage for rare victim phenotypes
- Generate coevolving polymorphism

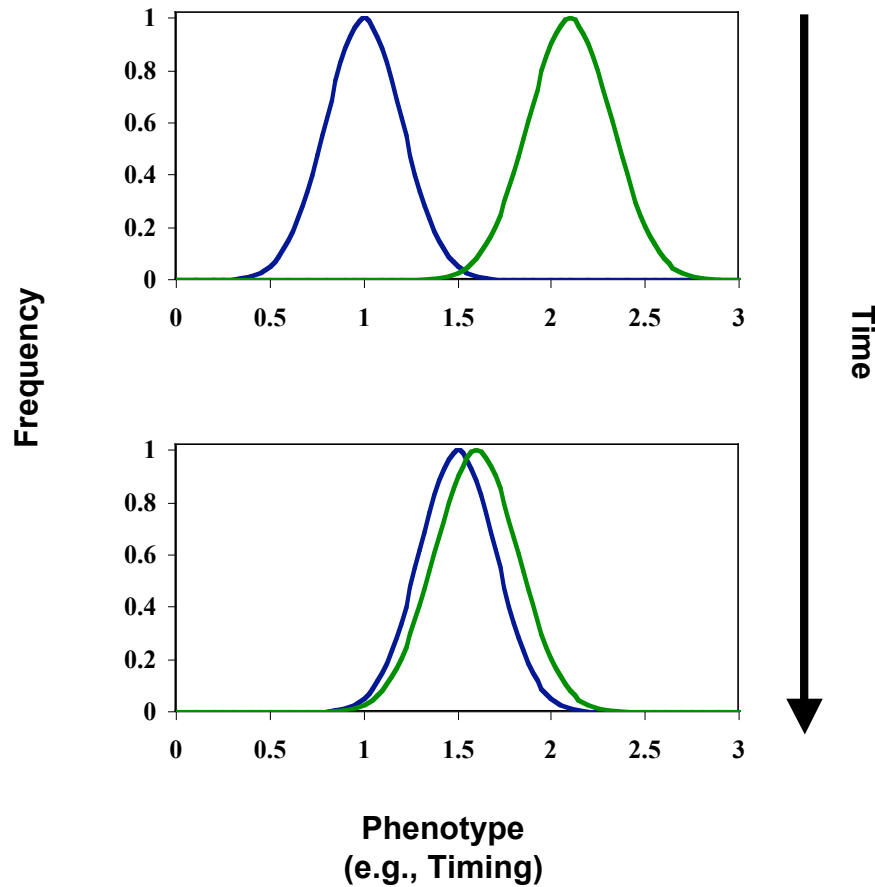
**Example:**

- Plant flowering time
- Insect emergence time
- Lice matching feather barb size



**MicroCoevolution**

**Coevolution in mutualistic interactions**



**Reciprocal Selection:**

- The fitness of Species 1 individuals is increased by interacting with Species 2 individuals
- The fitness of Species 2 individuals is increased by interacting with Species 1 individuals
- Reciprocal selection favors traits in both species that increase the efficacy or frequency of the interaction.
- Selection is positive frequency-dependent

**Coevolutionary dynamics:**

- Coevolving complementarity in symbiotic interactions.
- Coevolutionary convergence in free-living interactions.

**Modelos Genéticos microevolutivos**

Gen-for-Gen Coevolution

Table 1. *Matching allele model with n types (alleles). (+) indicates resistance in the host and (-) indicates susceptibility*

		host types			
		<i>R1</i>	<i>R2</i>	...	<i>Rn</i>
parasite types	<i>V1</i>	+	-	-	-
	<i>V2</i>	-	+	-	-
	...	-	-	+	-
	<i>Vn</i>	-	-	-	+

Matching allele

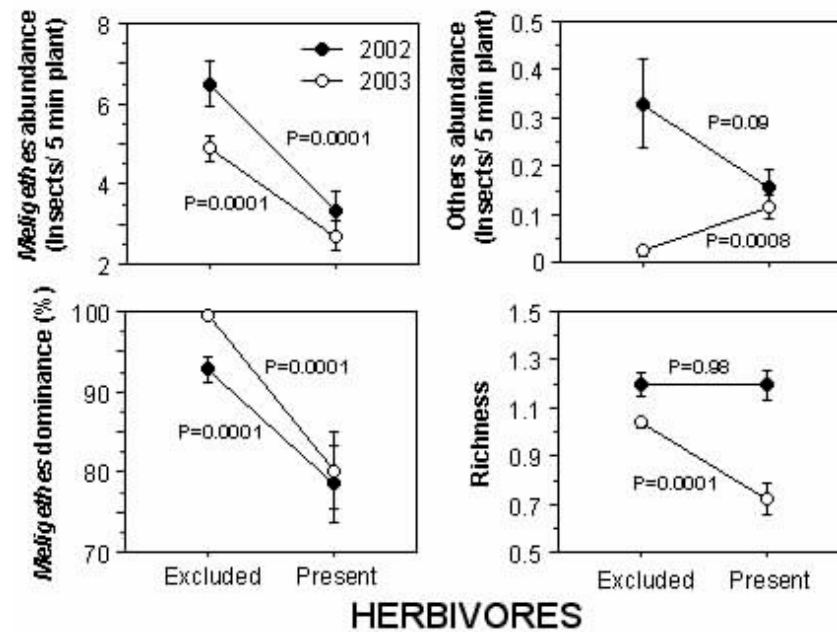
TABLE 1 The expected compatibility between homozygous genotypes in a single-locus gene-for-gene interaction

Pathogen genotype	Host genotype	
	<i>RR</i>	<i>rr</i>
<i>VV</i>	Incompatible	Compatible
<i>vv</i>	Compatible	Compatible

*R* is a dominant host gene conferring resistance to the pathogen and *r* is a recessive host gene conferring susceptibility. *V* is a dominant pathogen gene conferring avirulence and *v* is a recessive pathogen gene conferring virulence.

**Coevolución multispecifica o difusa**

- 1) La interacción con varios organismos esta genéticamente correlacionada.
- 2) La presencia/ausencia de otro organismo interactuante afecta a la interacción con nuestro organismo focal.
- 3) El impacto de un organismo en el fitness de su pareja se ve afectado por la presencia/ausencia de un tercer organismo

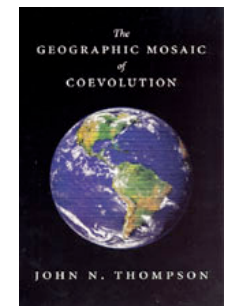


### **Geographic Mosaic Theory of Coevolution (GMTC)**

- a) Most species are formed by a collection of genetic and ecologically differentiated populations inserted in a complex landscape.
- b) The ecological interactions and community context varies spatially, among populations

The coevolutionary dynamics is driven by three main components

- 1) **Geographic selection mosaics:** Natural selection on interspecific interactions varies among populations.
- 2) **Coevolutionary hotspots:** Interactions are subject to reciprocal selection only within some local communities.
- 3) **Trait remixing:** The genetic structure of coevolving species changes through new mutations, gene flow across landscapes, random genetic drift, and extinction of local populations.



**Geographic Mosaic Theory of Coevolution (GMTC)**

This theory visualizes the landscape as a mosaic of coevolutionary hotspots, populations where reciprocal selection is strong and coevolution is ongoing, embedded in a broader matrix of coevolutionary coldspots, where local selection is weak, non-reciprocal or where only one of the participants occurs

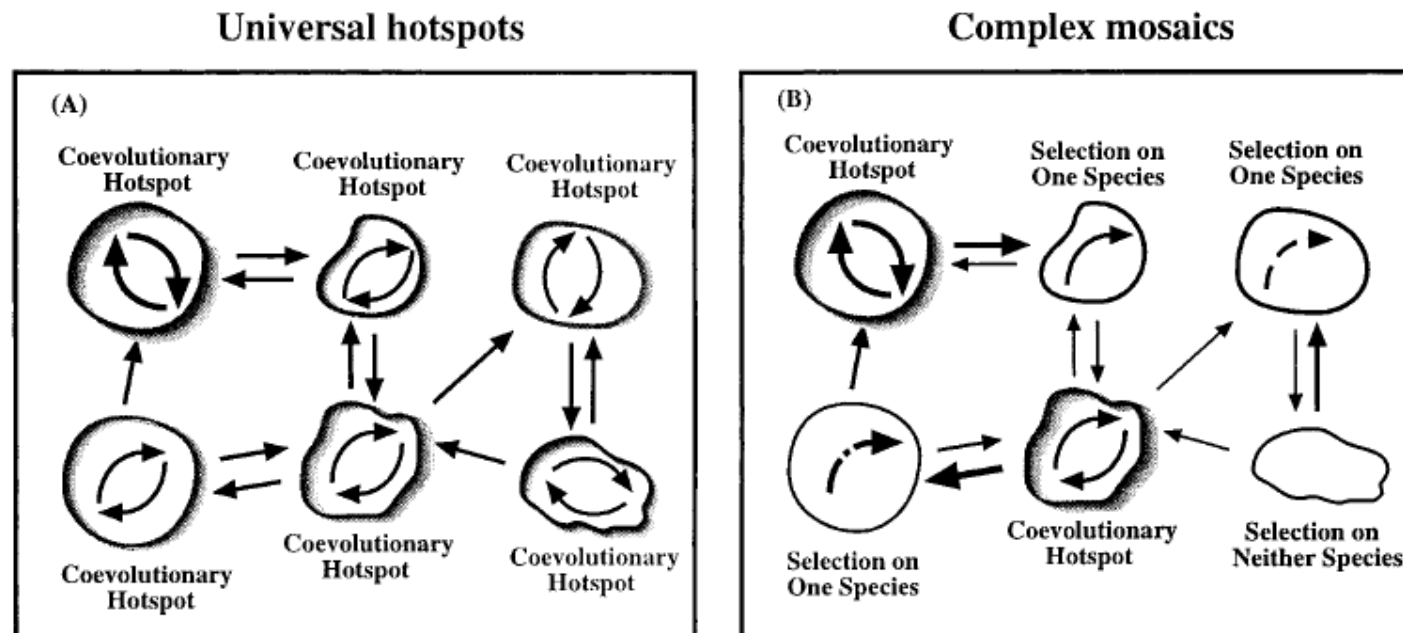
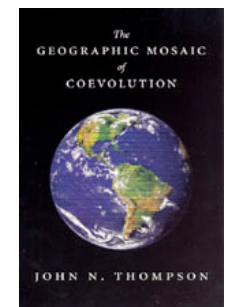
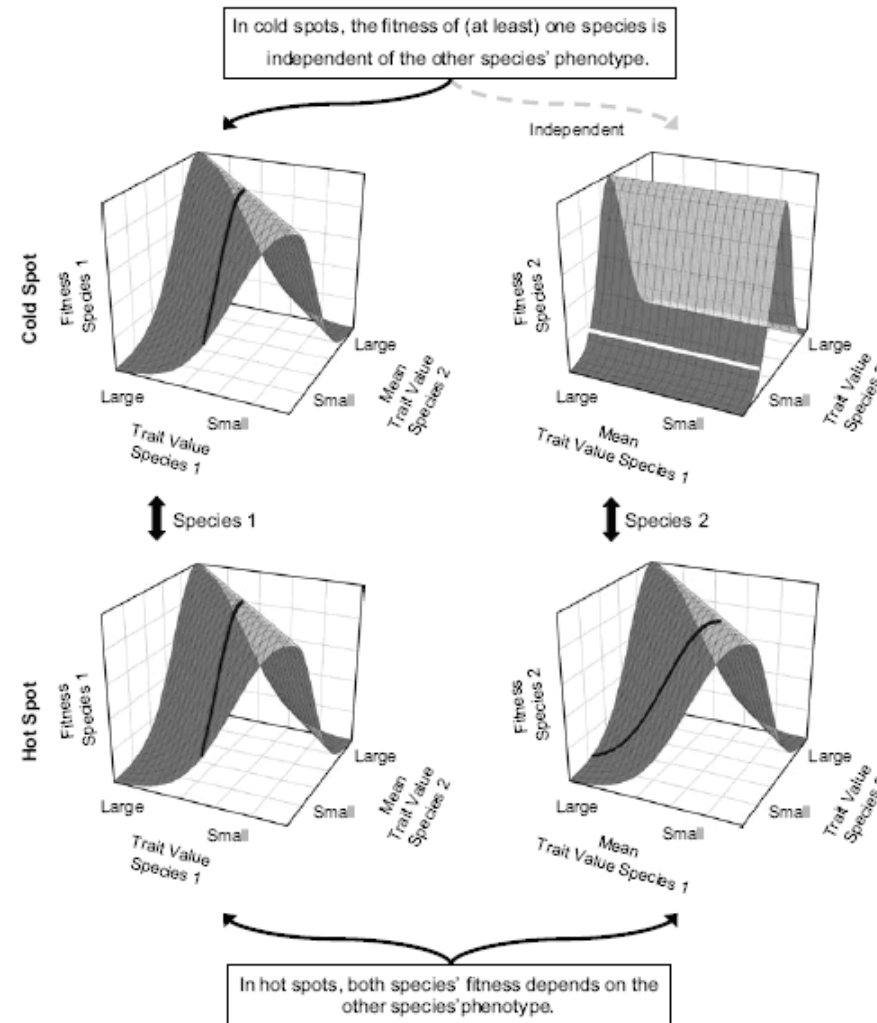


Figure 1: Hypothetical examples of a geographic mosaic of coevolution between a pair of species. Arrows within circles (biological communities) indicate selection on one or both species. Different arrow directions in different circles represent different (co)evolutionary trajectories. Arrows between communities indicate gene flow. A, Interaction coevolves in all populations in which it occurs; B, coevolutionary hot spots (i.e., communities in which reciprocal selection takes place) occur amid a matrix of coevolutionary cold spots.

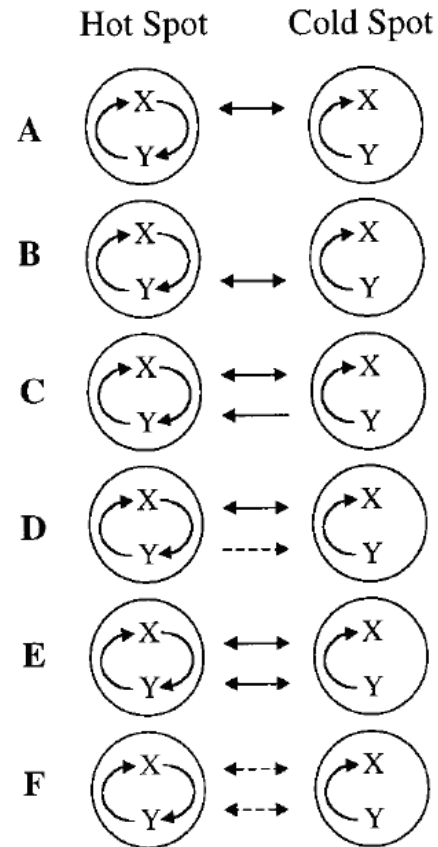


**Geographic Mosaic Theory of Coevolution (GMTC)**



**Figure 3** Interspecific frequency-dependent fitness surfaces in cold versus hot spots. Each point on a surface corresponds to the fitness of an individual of one species as a function of its own phenotype and the mean phenotype of the partner species with which it interacts. The thicker lines on each surface indicate the frequency-dependent fitness function for a particular phenotype of one species (left column: species 1 fitness functions; right column: species 2 fitness functions). In cold spots (top row), the fitness function of at least one species does not depend on the mean phenotype of the other species (top right, white line). Fitnesses of both species depend on the other species' mean phenotype in hot spots (bottom row).

**Geographic Mosaic Theory of Coevolution (GMTC)**



**Figure 1:** Types of coupled coevolutionary hot and cold spot habitats. Curved arrows indicate interspecific effects on fitness. The fitness of a species at the arrow tip is affected by the other species. Horizontal arrows indicate species-specific patterns of gene flow between hot and cold spots. Solid and dashed arrows indicate unlimited and limited levels of gene flow, respectively.



Un ejemplo

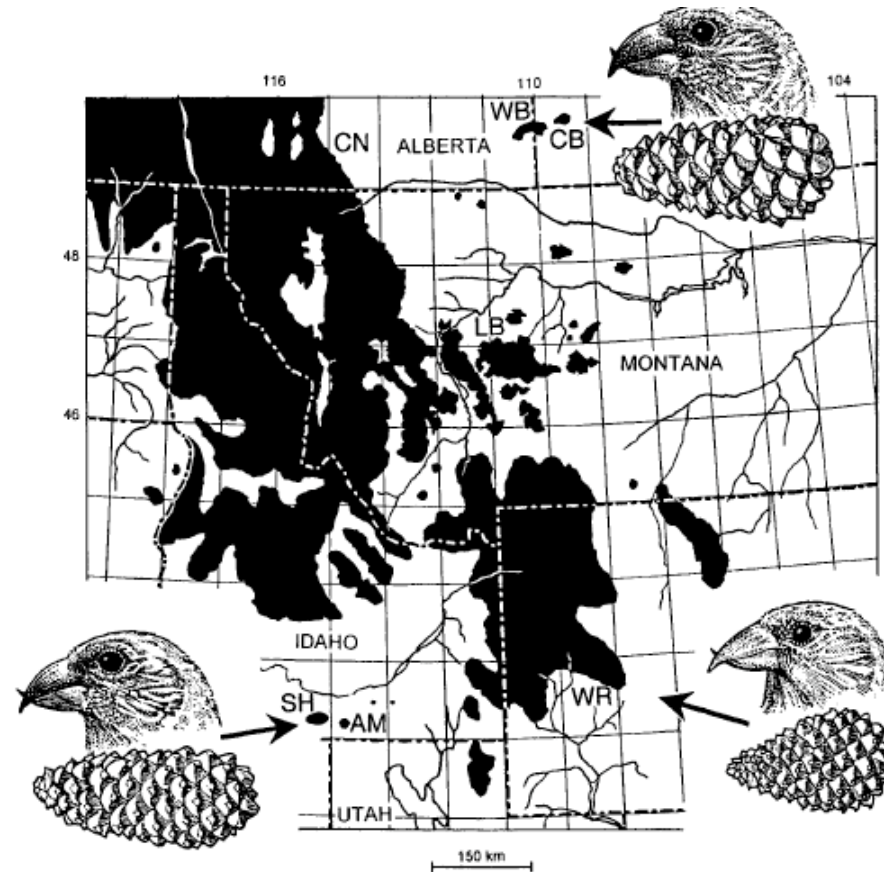


FIG. 1. The distribution of lodgepole pine (black), locations of study sites, and representative crossbills and cones in the Rocky Mountains (lower right), in the Cypress Hills (upper right), and in the South Hills and Albion Mountains (lower left; modified from Benkman 1999). The crossbills and cones are drawn to relative scale. Red squirrels (*Tamiasciurus hudsonicus*) are found throughout the range of lodgepole pine except in some isolated mountains, including the South Hills (SH) and Albion Mountains (AM). Red squirrels were absent from the West Block (WB) and Centre Block (CB) of the Cypress Hills until being introduced in 1950. One Rocky Mountain study site not shown was near Twin Lakes, Colorado approximately 650 km south-southeast of the Wind River Range (WR) site. The two other Rocky Mountain study sites were Crow's Nest Pass (CN) and Little Belt Mountains (LB).

## Modelos macro-coevolutivos

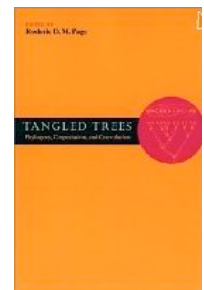
1 **Escape y radiación:** fenómenos de especiación sincrónicos en ambos participantes. Especiación ocurre cuando no hay interacción

2 **Coespeciación:** Existe especiación simultánea

3 **Coevolución diversificadora:** La propia interacción induce especiación como consecuencia de adaptación local recíproca

4 **Rastreo filogenético:** Un participante especia en función de la diversificación del otro participante

5 **Escalada:** El ambiente selectivo se hace más severo, induciendo cambios conjuntos en el fenotipo. Pero no hay proceso coevolutivo.



**Modelos macro-coevolutivos**

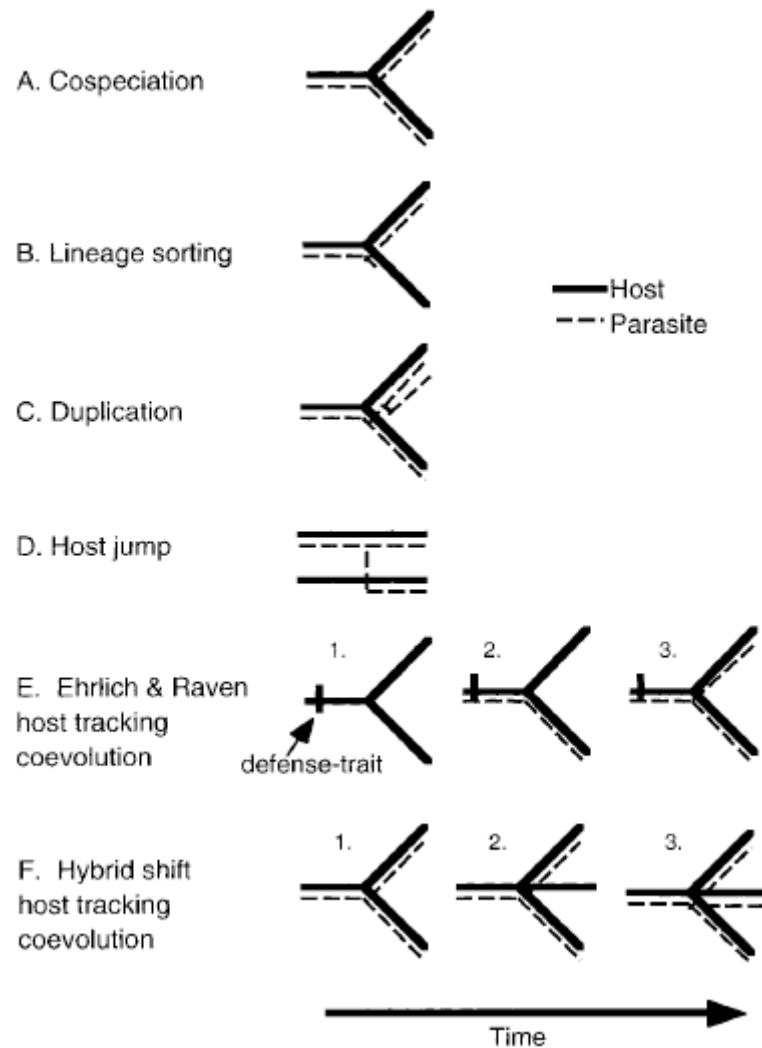
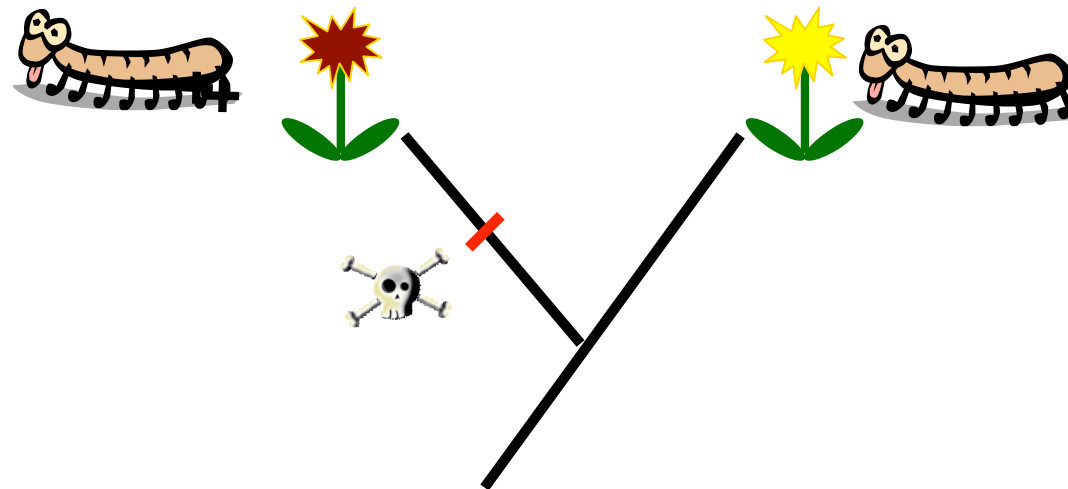


FIG. 1. Patterns of host-pathogen association. (A) Cospeciation: parasite and host speciate simultaneously. (B) Lineage sorting: here, a parasite lineage becomes extinct. (C) Duplication: the parasite splits into more than one species on the same host. (D) Host jump: the parasite jumps to a new, unrelated host species. (E) Ehrlich and Raven (1964) host-tracking coevolution: At time 1, a clade of hosts has no parasites because they are defended by a defense trait (at arrow). At time 2, a mutation has evolved in a parasite allowing it to attack a previously defended host species. By time 3, the parasite has colonized more related hosts and has also speciated on these hosts. (F) Hybrid shift host-tracking coevolution: At time 1, two host species are parasitized by different parasite species. At time 2, the host species have crossed to form a hybrid. By time 3, a parasite species exists that is capable of attacking the hybrids. Under both kinds of host tracking coevolution (E F), the parasites shift to closely related hosts.

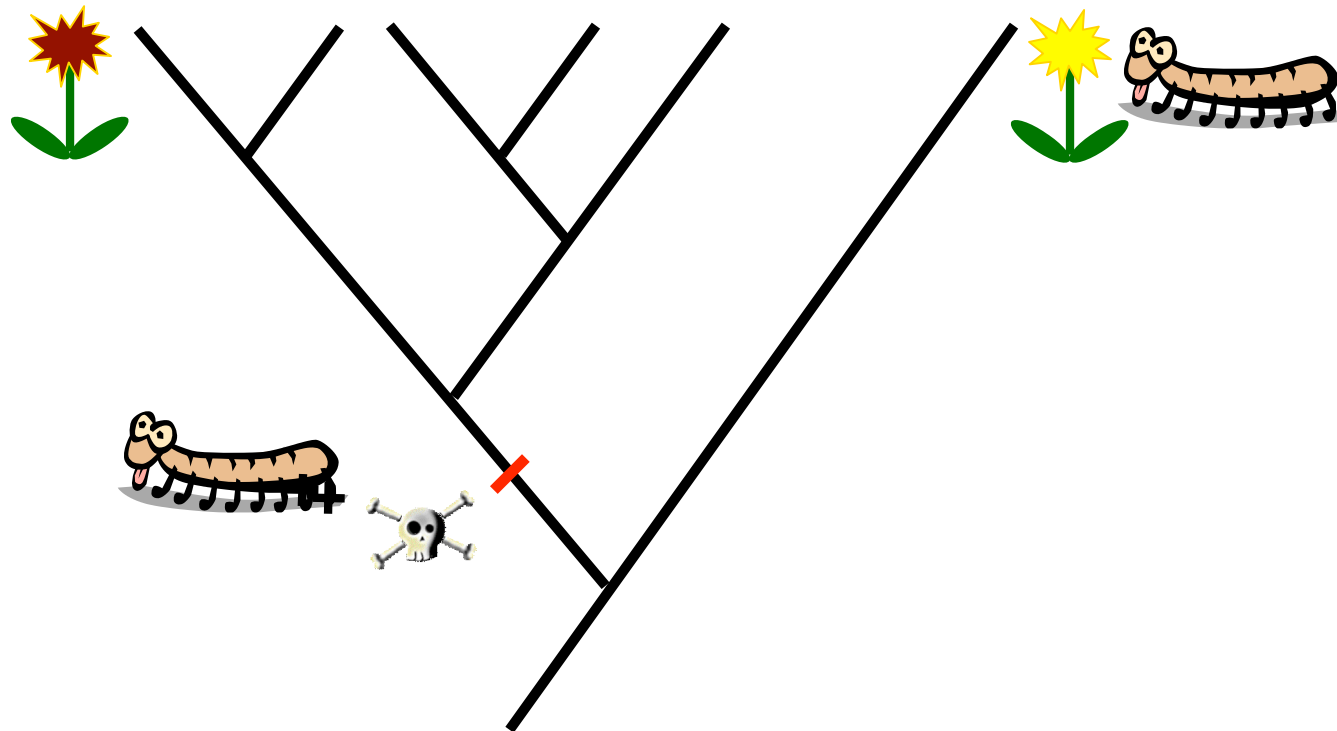
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Escape and radiation coevolution (Ehrlich and Raven 1964)



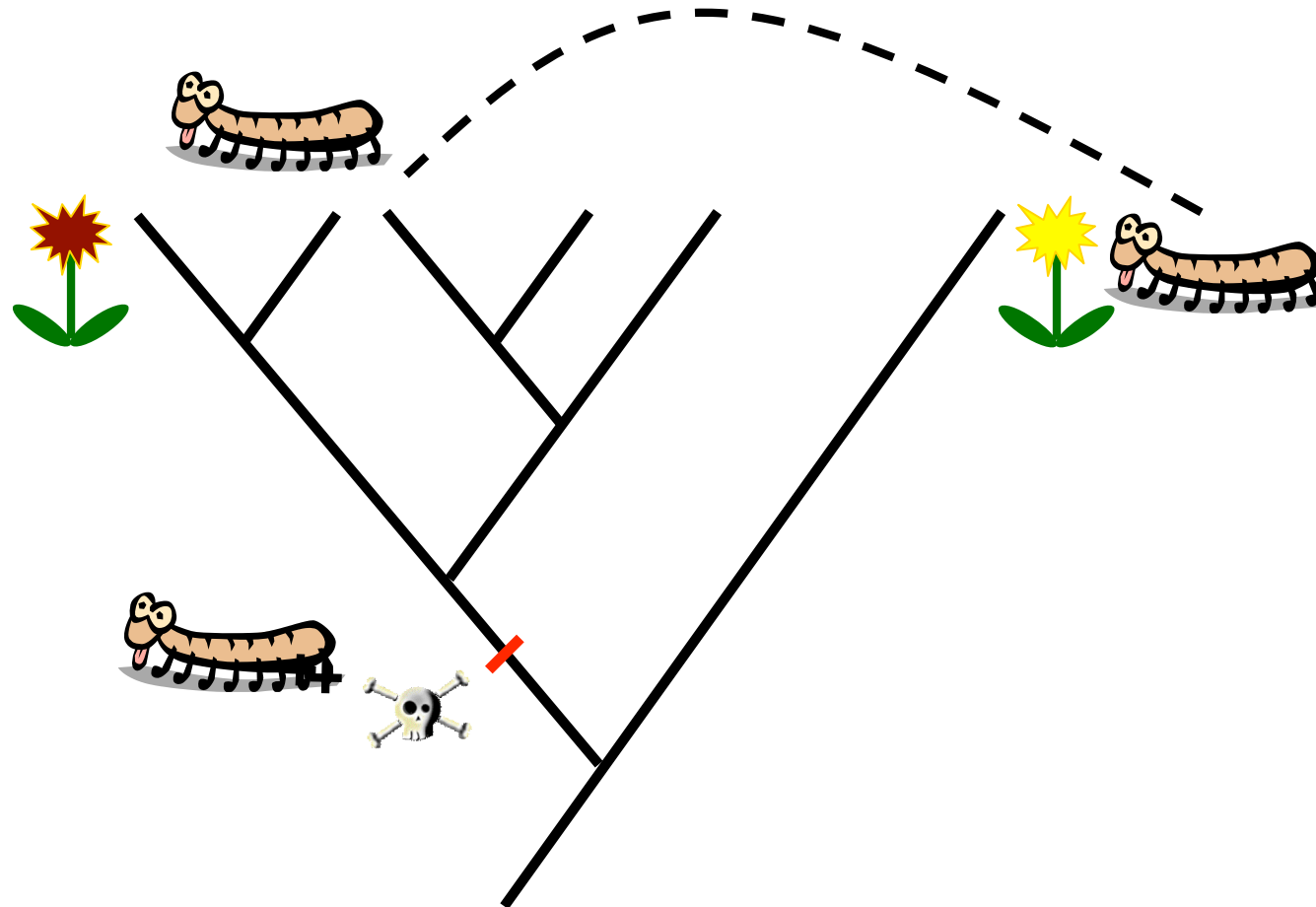
Step 1: A new mutation arises within a host (plant) lineage which confers resistance to parasitism

Escape and radiation coevolution (Ehrlich and Raven 1964)



Step 2: The resistant host lineage diversifies rapidly in the absence of parasitism

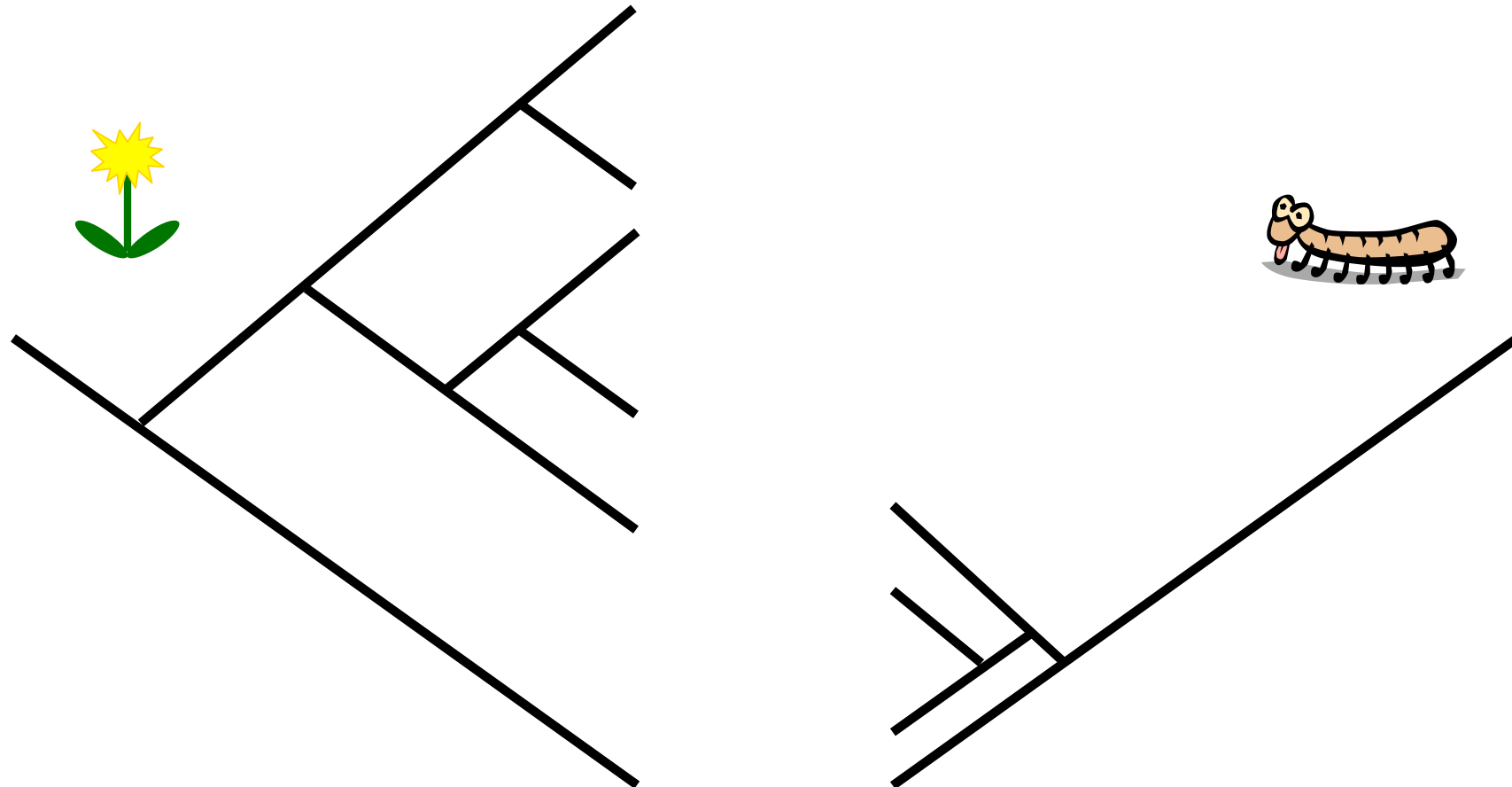
Escape and radiation coevolution (Ehrlich and Raven 1964)



Step 3: A new mutation arises in the parasite allowing it to feed on the previously resistant host lineages. Rapid parasite diversification follows.

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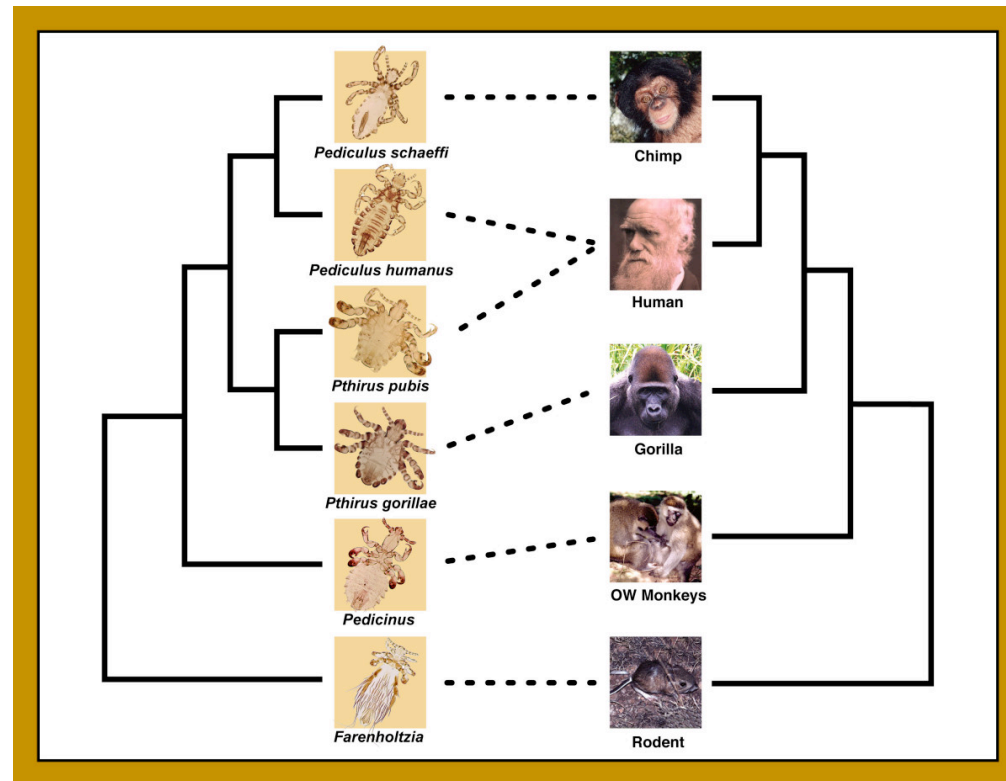
Escape and radiation coevolution (Ehrlich and Raven 1964)



The result is rapid bursts of diversification, but NOT cospeciation

**Escape and radiation coevolution (Ehrlich and Raven 1964)**

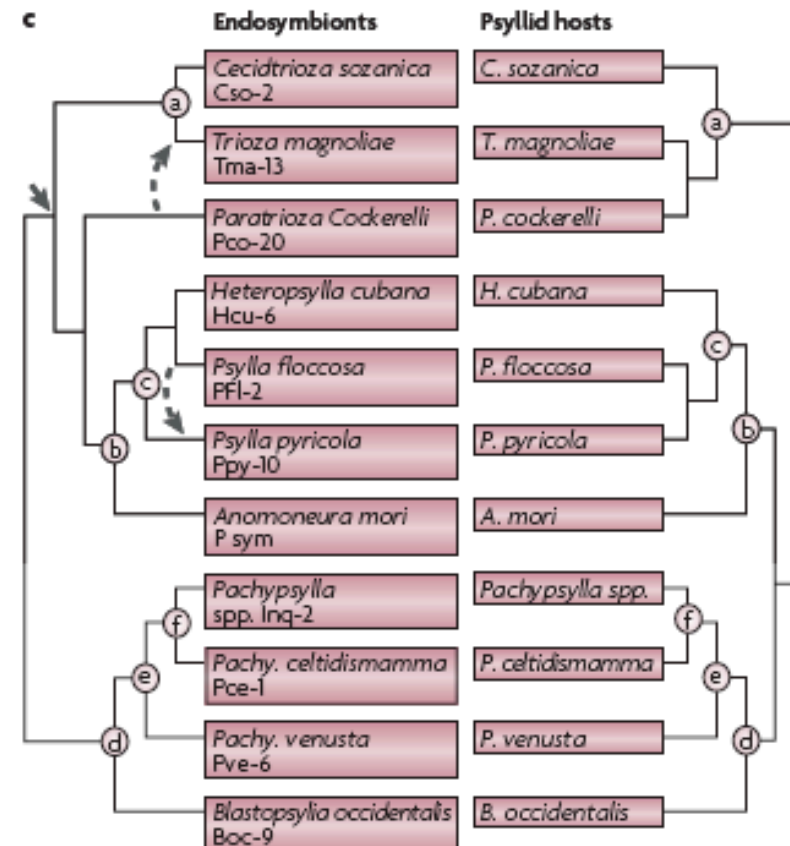
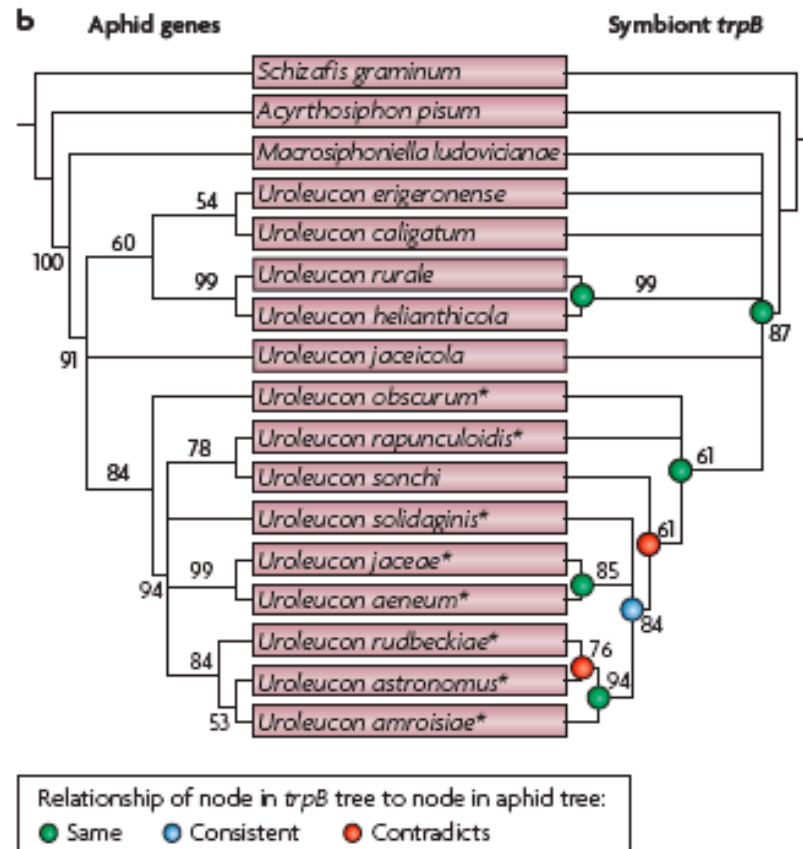
Esperamos congruencia filogenética





## Coespeciación

The parallel evolution of two associated taxa (such as a host and a symbiont), such that speciation events in the two taxa are coupled



## Host-shift and phylogenetic tracking in antagonism and mutualism

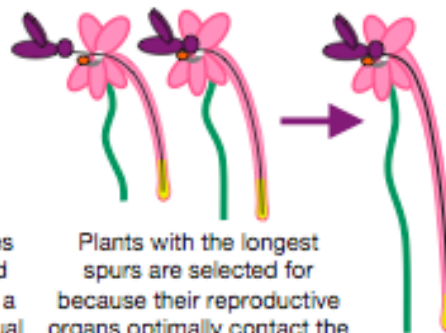
### a Darwin's coevolutionary race



Individuals with the longest tongues are selected for because they obtain the greatest food rewards

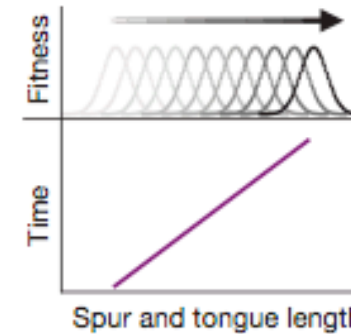


Selection alternates between plant and pollinator, causing a continual and gradual elongation of the pollinator's tongue and the flower's spur

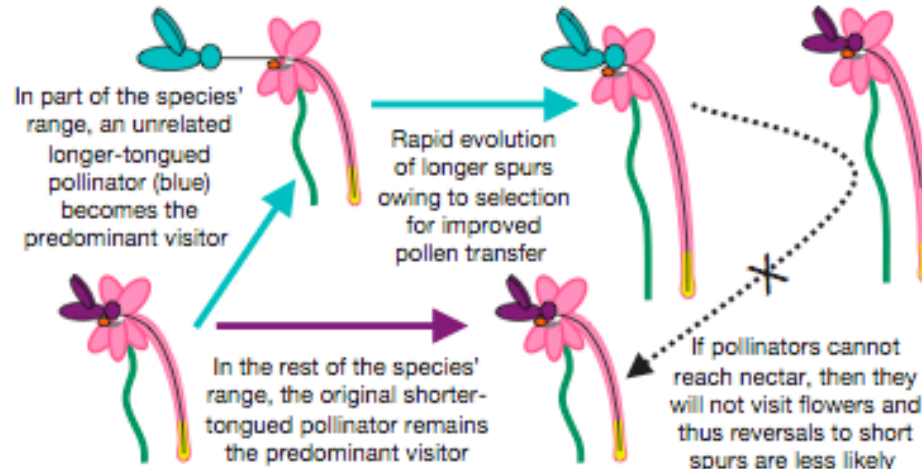


Plants with the longest spurs are selected for because their reproductive organs optimally contact the pollinators' body, providing the greatest reproduction

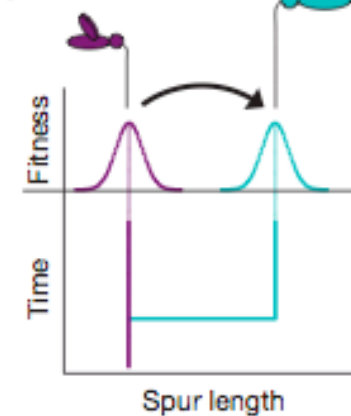
### b



### c Pollinator shift



### d



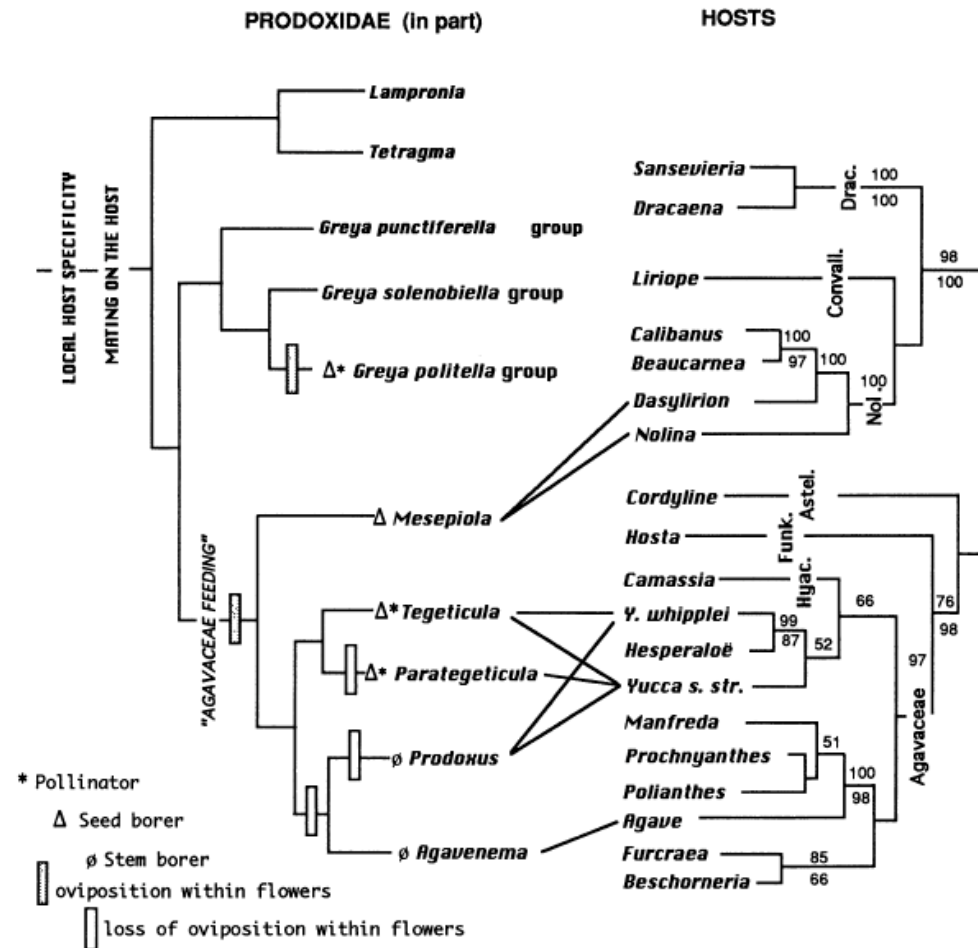


FIG. 1. Reduced phylogenies (for illustrative purposes only) of the Prodoxidae (16) and a suite of monocots (9, 12) most of which have been placed in the Agavaceae by various authors. The Prodoxidae phylogeny indicates that local host specificity and mating on the host are features that unite the family. The character "Agavaceae feeding" was considered by Pellmyr and Thompson (16) to define the yucca moths. The molecular phylogeny of Brown *et al.* (19) still recognized the existence of an Agavaceae feeding clade that consists of *Mesepiola* and its sister genera, but it placed the *Greya pollitella* group as a basal lineage of *Greya* and *Agavenema* within *Prodoxus*. The plant phylogeny on the right is that yielded from the combined ITS1 and ITS2 sequences. Bootstrap values >50% for the combined ITS data are given above the line and values for our cpDNA restriction site study are given below the line (17). The placements by Cronquist (9) and Dahlgren *et al.* (12) of the plant genera shown are shown in Table 1. Astel., Asteliaceae; Convall., Convallariaceae; Drac., Dracaenaceae; Funk., Funkiaceae; Hyac., Hyacinthaceae; Nol., Nolinaceae.

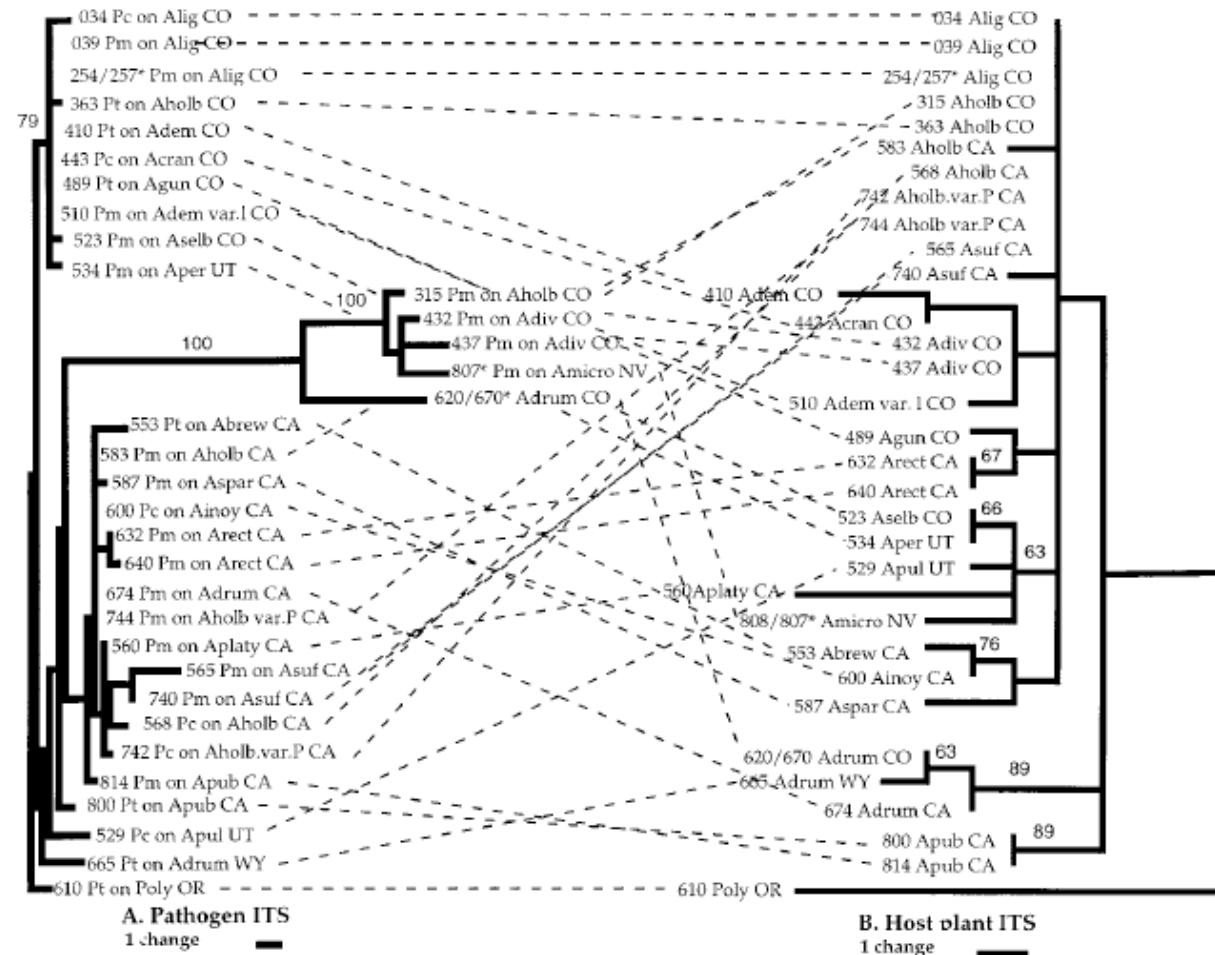
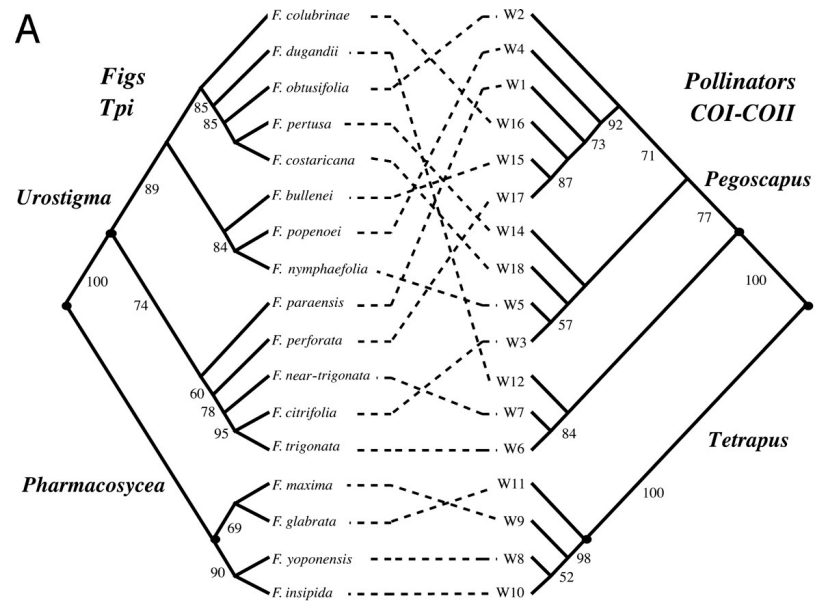
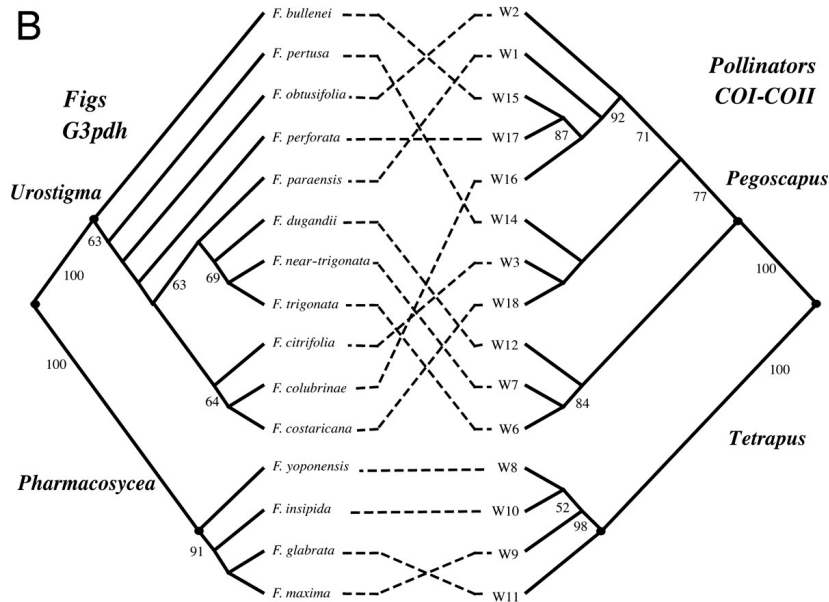


FIG. 4. Comparison of the rust fungus ITS phylogeny (A) with the host ITS phylogeny (B). The fungal species are abbreviated by Pt, Pm, and Pc, which represent *Puccinia thlaspeos*, *P. monoica*, and *P. consimilis*, respectively. Other abbreviations as in Figure 3. Collection numbers and host abbreviations correspond to the taxa listed in Table 1.



Why poor congruence of fig and fig wasp phylogenies?

- Multiple wasp species pollinating one fig species
- Host switching
- Evidence for frequent hybridization in figs but in wasps (inbreed)



Diversification of this mutualism has not occurred through strict-sense coadaptation and cospeciation between pairs of fig and wasp species