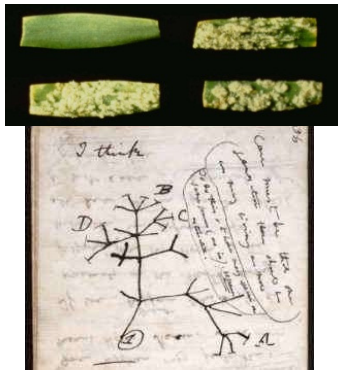
Application Evolution: Part 0.2
Coevolution

$$f_i = \frac{\theta}{i}\binom{n-1}{i}^{-1}\sum_{k=2}^{n-i+1}\binom{k}{2}\binom{n-k}{i-1}E(T_k), \quad 1 \le i \le n-1.$$

S. chilense



S. peruvianum

$$E(T_k) = \sum_{j=k}^{n}(-1)^{j+k}\frac{(2j-1)n!(n-1)!(j+k-2)!}{k!(k-1)!(n-j)!(n+j-1)!(j-k)!}\int_0^\infty \exp\left(-\beta_1^2\binom{j}{2}\int_0^t 1/\rho(s)ds\right)dt.$$

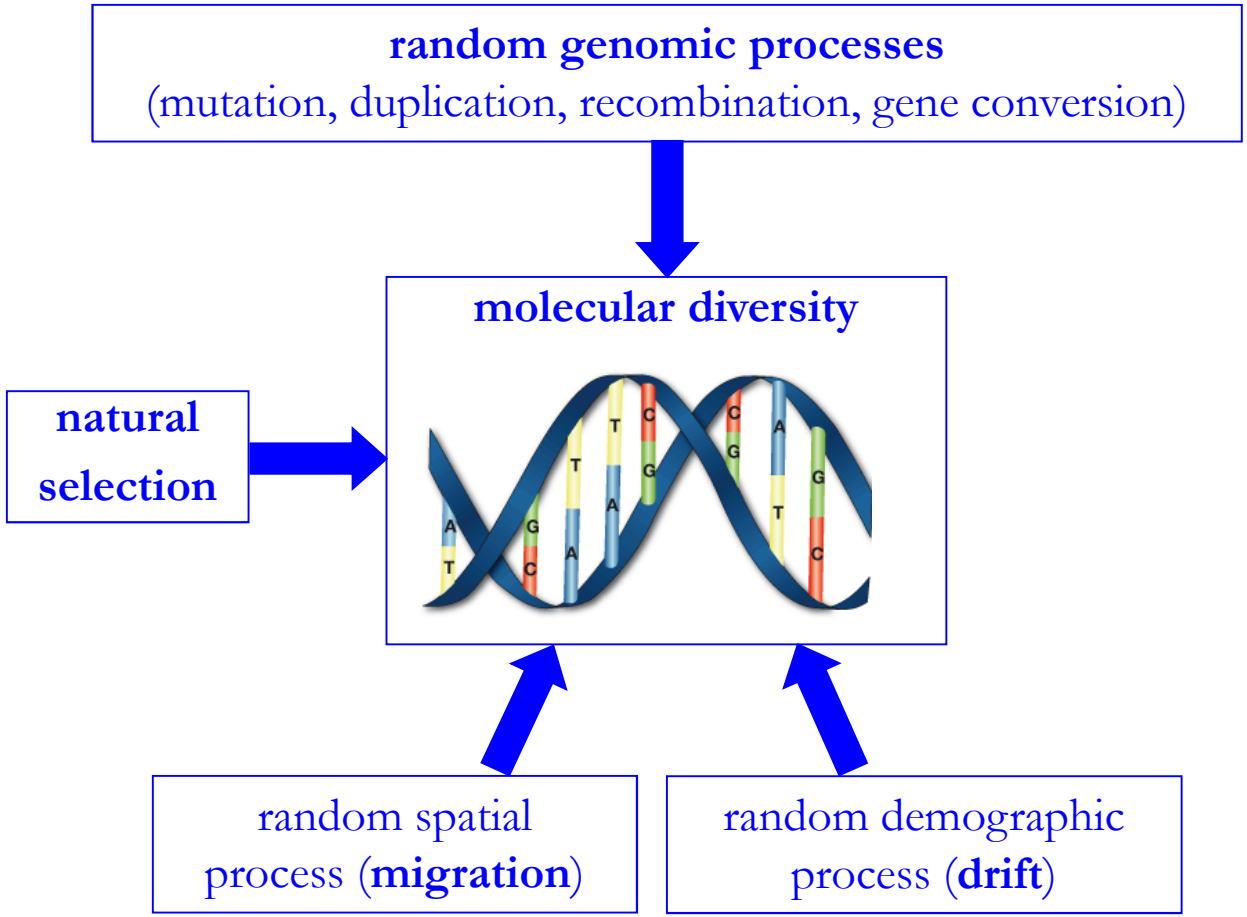
Summer Semester 2013

Prof Aurélien Tellier

FG Populationsgenetik

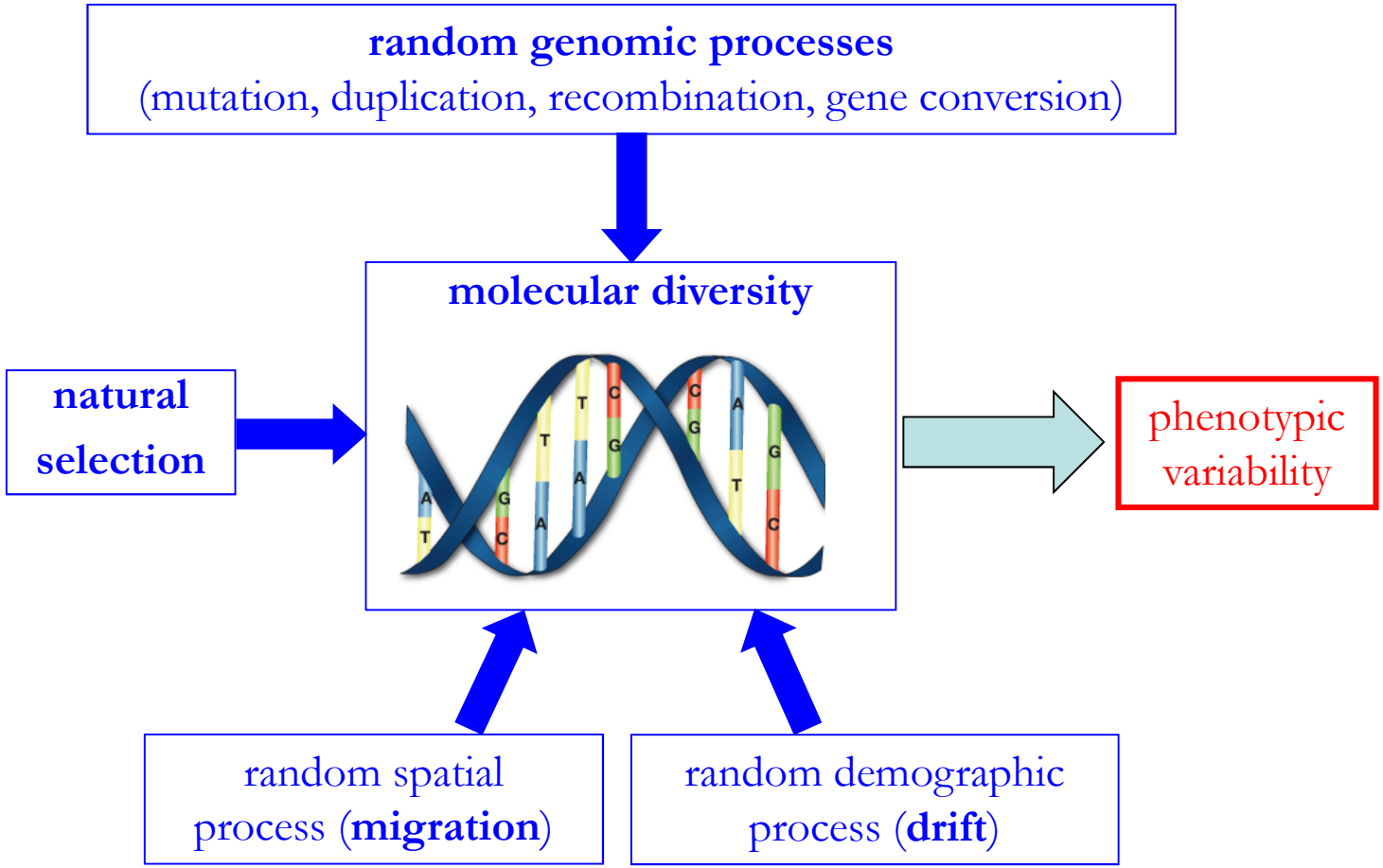
Technische Universität München

Population genetics: 4 evolutionary forces



Population genetics investigates the laws governing the genetic structure of populations, and changes in allele frequencies over time

Population genetics: 4 evolutionary forces



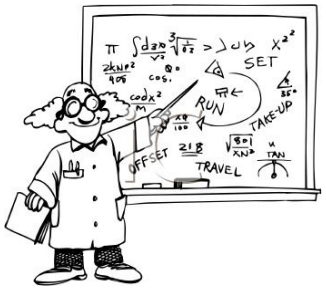
Color code

Color code:

Red = Important result or definition

Purple: exercise to do

Green: some bits of maths



Definition coevolution

Evolution = changes between generations of frequency of characters, traits or alleles

Coevolution = reciprocal changes between generations of frequency of characters, traits or alleles in hosts and parasites

coevolution is defined as **evolution in two or more evolutionary entities brought about by reciprocal selective effects between the entities.**

Definition coevolution

- coevolution can occur if part of the environment of a species is shaped by a specific set of genes of one or several other species the intensity (i.e. the fitness effects) and frequency (i.e. the spatial and temporal patterns) of the interaction are important parameters for coevolution

- only if both parameters are high do we expect highly specialised

- interactions to coevolve
  - otherwise the interactions can be quite diffuse (but they may nevertheless sometimes also lead to big effects)

- extended phenotype all effects of a gene upon the world. As always, 'effect' of a gene is understood as meaning in comparison with the other alleles
  - the ‘conventional’ phenotype is a special case in which the effects are regarded as being confined to the individual body in which the gene sits

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Definition coevolution

- involved frequency dependent selection between two types of players in an **evolutionary "game"**. The "game theory" underlying this idea could be either between species (as in interspecific competition) or within species (different morphs of the same species) competing for a resource

- coevolutionary interactions can be classified in the following types:

mutualism (+/+)
parasite-host, predator-prey (+/-)
competition (-/-)

} narrow-sense coevolution: both partners evolve in response to the other

commensalism (0/+)
by-product (0/-)

} broad-sense coevolution only one of the partner evolves in response to the other

Definition coevolution

Types of coevolution

In ***specific coevolution***, or ***coevolution in the narrow sense***, in which one species interacts closely with another, and changes in one species induce adaptive changes in the other, and vice-versa. **In some cases, this adaptation may be polygenic; in other cases, there may be *gene-for-gene coevolution*, in which the mutual interactions are between individual loci in the two species.**

Specific coevolution may of course be short-lived, but if the interaction is very close, as in many host-parasite systems, ***concordant speciation*** or ***cospeciation*** may result; where the speciation in one form causes speciation in another. Of course, cospeciation doesn't necessarily require coevolution. For example, a very unimportant but highly host-restricted parasite may always speciate whenever its host speciates, without the parasite causing any evolutionary reaction in the host.

Definition coevolution

Cospeciation

New Phytologist

Review

Tansley review

Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution

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Definition coevolution

Types of coevolution

In ***diffuse coevolution***, also called ***guild coevolution,*** whole *groups of species* interact with other groups of species, leading to changes that cannot really be identified as examples of specific, pairwise coevolution between two species. For example, a group of plant species may be fed on by a particular family of insects, which may frequently (in evolutionary time) change hosts. The plants may evolve defensive adaptations, such as defensive chemistry, or physical defenses such as spines, which work against large numbers of the species. In time, some of the insects may be able to overcome the plant's defences, leading to further evolution by the plant, and so on.

Definition coevolution

- the costs and benefits of the interactions between the partners can be difficult to measure and they may depend on the environment

- the interactions may vary spatially and temporally
  - a species may coevolve with another species over only part of its range and/or
  - only part of the time
  - complete spatial and temporal overlap is unlikely the condition at the origin of an interaction and not the most frequent case

- similar life histories facilitate coevolution between partners

- the interactions may vary in symmetry

- understanding the signs and strengths of coevolutionary interactions may require sampling over several populations
  - and thus gene flow between these populations is important

Definition coevolution

- levels of coevolution
  - genetic elements within organisms
  - ancient symbioses
  - males and females
  - parents and offspring
  - coevolving species
  - coevolving clades
  - coevolution of genes and culture
  - coevolution can be inter- or intra-specific

Examples of coevolution

Plants and pollinators

- the star orchid (*Angraecum sesquipedale*) from Madagascar has an extremely long floral tube (28-32 cm)
- based on its examination Darwin in 1862 hypothesised that this floral tube had evolved as a consequence of coevolution
- he predicted that there must exist a moth with similarly long proboscis
- his suggestion was ridiculed by entomologists

From: A Very Victorian Passion: The Orchid Paintings of John Day.

Examples of coevolution

Plants and pollinators

- a candidate hawkmoth (*Xanthopan morganii praedicta*) was described in 1903 but the first observations of the actual pollination behaviour were made only recently

Figure 2.8 The Madagascar star orchid (*Angraecum sesquepedale*) is pollinated by a hawkmoth (*Xanthopan morgani praedicta*) whose existence and long proboscis were predicted by Darwin from the morphology of the orchid. The length of the orchid's nectary has evolved to fit the length of the hawk's proboscis. (Photo courtesy of L. T. Wasserthal.)

from Stearns & Hoekstra 2005

Examples of coevolution

Plants and pollinators

- in another orchid species (*Plathanthera bifolia*) the floral tube length does affect the reproductive success
  - so tubes that accommodate the entire tongue are advantageous for the orchids because they lead to more efficient pollen transfer

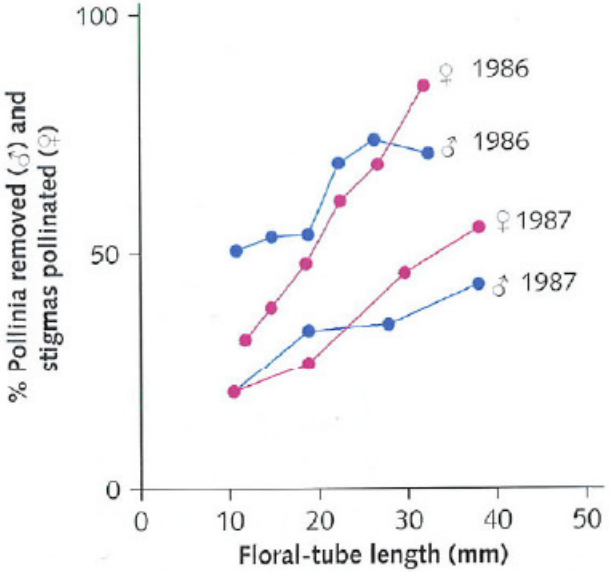


Figure 2.9 The sexual performance of a species of Swedish orchid, *Platanthera bifolia*, as a function of the lengths of its floral tubes. The longer the tubes, the more pollinia were removed and more stigmas were pollinated. Experiments were performed on two different years, 1986 and 1987. (From Nilsson 1988, reproduced by kind permission of the author and *Nature*.)

from Stearns & Hoekstra 2005

Examples of coevolution

Plants and pollinators

- so why should an exaggerated floral tube length evolve?
  - the moths may evolve a longer tongue than needed to forage efficiently
    - pollen transfer could carry costs
    - close contact to the flower due to a matching tongue length could lead to higher predation on moths by ambush predators that sit on the flowers
  - there must be a benefit for the orchid if the moth has a too short tongue
    - does it pay for the orchid to cheat by economising on nectar?
    - is the pollen export improved if the moth has to try harder?

Examples of coevolution

Batesian mimicry

- in Batesian mimicry an edible species (the mimic) evolves to resemble a warningly coloured noxious species (the model)
- selection on Batesian mimicry is mediated by predators that avoid mimics because they are trying to avoid the models
- the convergence of the mimic to the model is limited by the sensory system of the predator
  - thus the fact that many mimics are quite accurate copies of their models suggests that predators have sophisticated sensory systems
- the cost of eating a model must be higher than be benefit of eating a mimic
- may lead to the evolution of learning in the predator
- the fitness advantages for the mimic are frequency-dependent
- has evolved many times independently

Examples of coevolution

Batesian mimicry

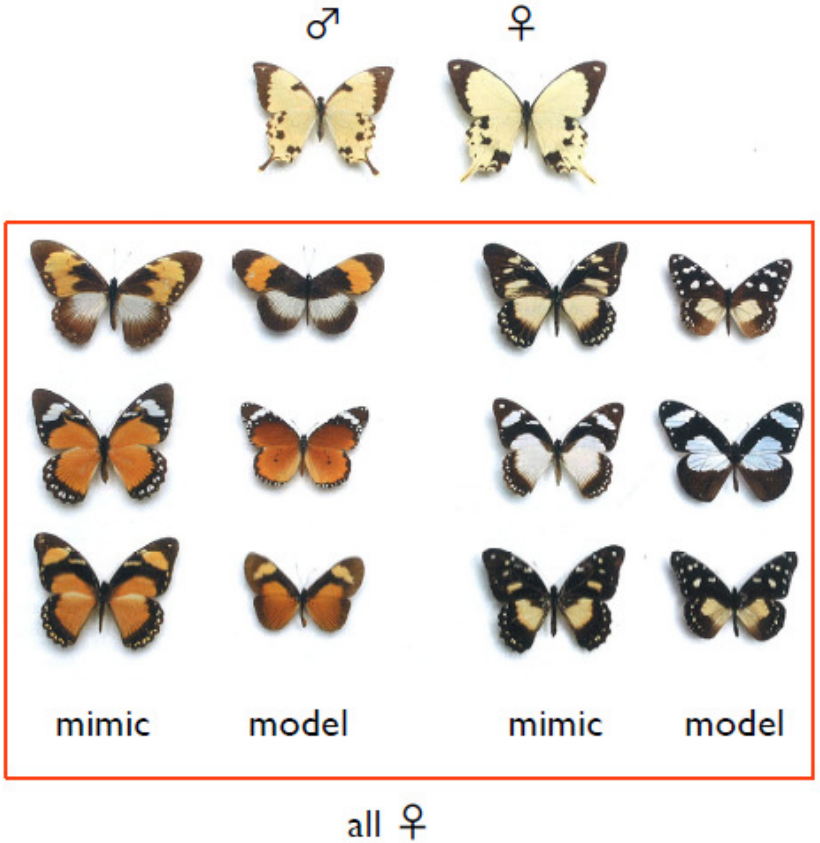


Figure 18.6 The mocker swallowtails of Africa (*Papilio dardanus*) are one of the most remarkable cases of Batesian mimicry known. The females mimic different toxic models in different geographical regions, with the result that they look very different both from the males of their own species and from the females of their species in other geographical regions. The males are not mimics, and on Madagascar, where no toxic models are available, the females are not mimics and resemble the males. Top row: Left, male; right, female from Madagascar. In the remaining rows the mimicking female is on the left and the toxic model is on the right of each pair. Second row: left pair, left specimen, *P. dardanus* var. *planemoides* female (mimic); right specimen, *Bematistes poggei* (model) from Kenya; right pair, left specimen, *P. dardanus* var. *trophonius* female (mimic); right specimen, *Danaus chrysippus* (model) from South Africa. Third row: left pair, left specimen, *P. dardanus* var. *niobe* female (mimic); right specimen, *Bematistes tellus* (model) from Sudan; right pair, left specimen, *P. dardanus* var. *hippocoonides* female (mimic); right specimen, *Amauris albimaculata* (model) from Mozambique. Fourth row: left pair, left specimen, *P. dardanus* var. *hippocoon* female (mimic); right specimen, *Amauris naivius naivius* (model) from Great Lakes region; right pair, left specimen, *P. dardanus* var. *cenea* female (mimic); right specimen, *Amauris echeria* (model) from South Africa. The models are in the family Nymphalidae; the mimics are in the family Papilionidae. The papilionid mimics accurately reproduce the patterns that evolution elicits from the nymphalid ground plan (Figure 7.2). (Butterfly photos credit to Terry Dagradi; specimens courtesy of the Peabody Museum, Yale University, arranged by Raymond Pupedis, Curatorial Assistant in Entomology.)

Examples of coevolution

- ***Predator-prey coevolution***

- Predators have obviously evolved to exploit their prey, with hunting ability being at a premium. Mammalian predators, for example, must be fast, strong and cunning enough to be able to catch their prey. It is almost as obvious that prey have evolved to protect themselves from predators.

- They may have a variety of defenses:
  - Large size and strength
  - Protective coverings such as shells or hard bony plates
  - Defensive weapons, such as stings or horns
  - Defensive coloration (see mimicry lecture)
  - Unpalatability and nastiness

Examples of coevolution

Two of the most famous are figs and fig-wasps, and *Yucca* and Yucca moths (*Tegeticula*).

In both cases, the larvae are seed/flower eaters, which reduce the fertility of the flowers or inflorescences they infest.

In both cases, the plant is completely dependent on its herbivore for pollination. The arrangement is therefore a tightly coevolved mutualism, in which the plant relies exclusively on the insect for pollination, and the insect relies exclusively on the plant for food.

In the case of the Yucca moth the mutualism has sometimes broken down, and some clades of the moth have reverted to a parasitic mode of life -- they oviposit in the plant, but do not pollinate -- the ancestral condition for the moths.

These examples are interesting because they represent cases where mutualisms have become so specific that they almost rival the ancient prokaryotic mutualisms of mitochondria and chloroplasts with archaebacterial cells, to produce what we now know as eukaryotes

Examples of coevolution

Importance in agriculture and for human health

Interactions host-parasites

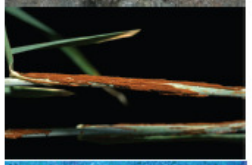
- Examples of new emergent diseases on animals and plants

Emerging fungal threats to animal, plant and ecosystem health

Matthew C. Fisher[1], Daniel. A. Henk[1], Cheryl J. Briggs[2], John S. Brownstein[3], Lawrence C. Madoff[4], Sarah L. McCraw[5] & Sarah J. Gurr[5]

The past two decades have seen an increasing number of virulent infectious diseases in natural populations and managed landscapes. In both animals and plants, an unprecedented number of fungal and fungal-like diseases have recently caused some of the most severe die-offs and extinctions ever witnessed in wild species, and are jeopardizing food security. Human activity is intensifying fungal disease dispersal by modifying natural environments and thus creating new opportunities for evolution. We argue that nascent fungal infections will cause increasing attrition of biodiversity, with wider implications for human and ecosystem health, unless steps are taken to tighten biosecurity worldwide.

Table 1 | Major fungal organisms posing threats to animal and plant species.

	Host	Pathogen (Phylum)	Disease dynamics leading to mass mortality in animal and plant hosts
	Amphibian species (for example, the common midwife toad, *Alytes obstetricans*)	*Batrachochytrium dendrobatidis* (Chytridiomycota)	Worldwide dispersal of a hypervirulent lineage by trade[64]. Ultra-generalist pathogen manifesting spillover between tolerant/susceptible species. Extent of chytridiomycosis is dependent on biotic and abiotic context[16,62].
	Rice (*Oryza sativa*); *Magnaporthe grisea* species complex on 50 grass and sedge species, including wheat and barley	*Magnaporthe oryzae* (Ascomycota)	Rice blast disease in 85 countries, causing 10–35% loss of harvest. Global blast population structure determined by deployment of seeds with inbred race-specific disease resistance (RSR). Invasions occur by 'host hops' and altered pathogen demographics.
	Bat spp. (little brown bats, *Myotis lucifugus*)	*Geomyces destructans* (Ascomycota)	New invasion of North American bat roosts occurred in approximately 2006, and disease is spreading rapidly[8]. Pathogen reservoir may exist in cave soil. Disease is more aggressive compared to similar infections in European bats, possibly owing to differences in roosts and host life histories[65].
	Wheat (*Triticum aestivum*); 28 *Puccinia graminis* f. *tritici* species, but *P. graminis* is found on 365 cereal or grass species	*Puccinia graminis* (Basidiomycota)	Wheat stem rust is present on six continents. Population structure is determined by deployment of RSR cultivars and long-distance spread of aeciospores. Strain Ug99 poses a notable threat to resistant wheat varieties, causing up to 100% crop loss.
	Coral species (for example, the sea fan, *Gorgonia ventalina*)	*Aspergillus sydowii* (Ascomycota)	Sea-fan aspergillosis caused by a common terrestrial soil fungus[21,66]. Epizootics are associated with warm-temperature anomalies. Coral immunosuppression is probably a factor causing decline.
	Bee species (for example, the hive of the domestic honeybee (*Apis mellifera*) suffering colony collapse disorder)	*Nosema* species (Microsporidia)	Microsporidian fungal infections are associated with colony collapse disorder and declining populations. Pathogen prevalence is probably a part of a multifactorial phenomenon that includes environmental stressors and polyparasitism[67,68].
	Sea turtle species (the loggerhead turtle, *Caretta caretta*)	*Fusarium solani* (Ascomycota)	Soil-dwelling saprotroph and phytopathogenic fungus. Infection causes hatch failure in loggerhead turtle nests and suboptimal juveniles[69]. The disease dynamics fulfil Koch's postulates. Environmental forcing is suspected but not proven.

Images in Table 1, with permission: *A. obstetricans* chytridiomycosis mortalities, M.C.F.; *M. oryzae*, N. Talbot; WNS-affected little brown bats, A. Hicks; *P. graminis*, R. Mago; *G. ventalina* infected with *A. sydowii*, D. Harvell; *A. mellifera* hive suffering from colony collapse disorder, J. Evans; sea turtle eggs infected with *F. solani*, J. Delgado-Uribeondo and A. Marco.

Interactions host-parasites

- Examples of plant-parasite coevolution

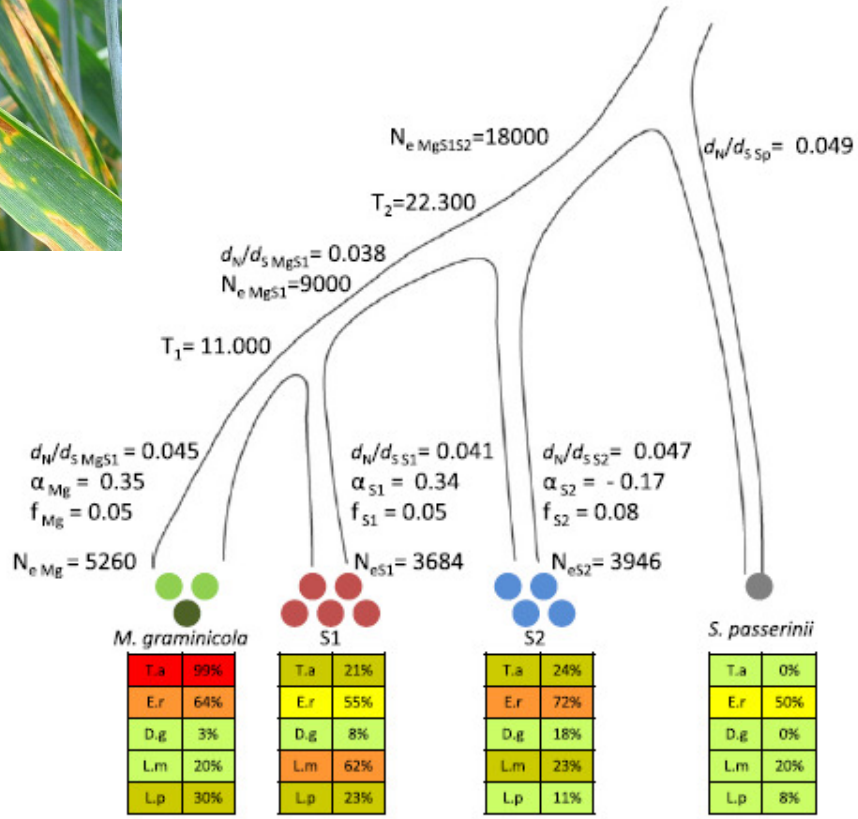


Figure 1. Species tree of *M. graminicola*, S1, S2, and *S. passerinii*. Circles indicate the number of genomes sequenced in each species. In our analyses we used the reference sequence of *M. graminicola* marked as a dark green circle. The *lower* panels of the figure summarize the ability of each species to infect the five grass species (T.a.) *Triticum* aestivum, (E.r.) *Elymus repens*, (D.g.) *Dactylis glomerata*, (L.m.) *Lolium multiflorum*, and (L.p.) *Lolium perenne*. The extent of host adaptation was estimated as percentage of leaf area covered by pycnidia among the different host species. Colors corresponding to the degree of infection are shown as 0%–20% (light green), 21%–40% (brownish green), 41%–60% (yellow), 61%–80% (orange), 81%–100% (red). We used a coalescence approach to estimate the split between *M. graminicola* and S1 (T_1) and the more ancient split between S2 and the *M. graminicola*-S1 branch (T_2). The population sizes of the ancestral species are indicated as N_{eMgS1} and $N_{eMgS1S2}$ parameters. The evolutionary rate is estimated as the ratio of nonsynonymous to synonymous mutation rates d_N/d_S for each branch. Shown are also estimates of the parameter α quantifying the extent of adaptive evolution and the parameter *f* as a measure of the strength of purifying selection in each of the branches of *M. graminicola*, S1, and S2 using *S. passerinii* as the outgroup species. Contemporary effective population sizes were estimated from polymorphism data for each species and are given as N_{eMg}, N_{eS1}, and N_{S2}.

Stuckenbrock *et al.* 2011, Evolution of *Mycosphaerella graminicola* pathogen of wheat

Interactions host-parasites

- Horizontal gene transfer from one species to another: ex of virulence factors in parasite to favor host-jump

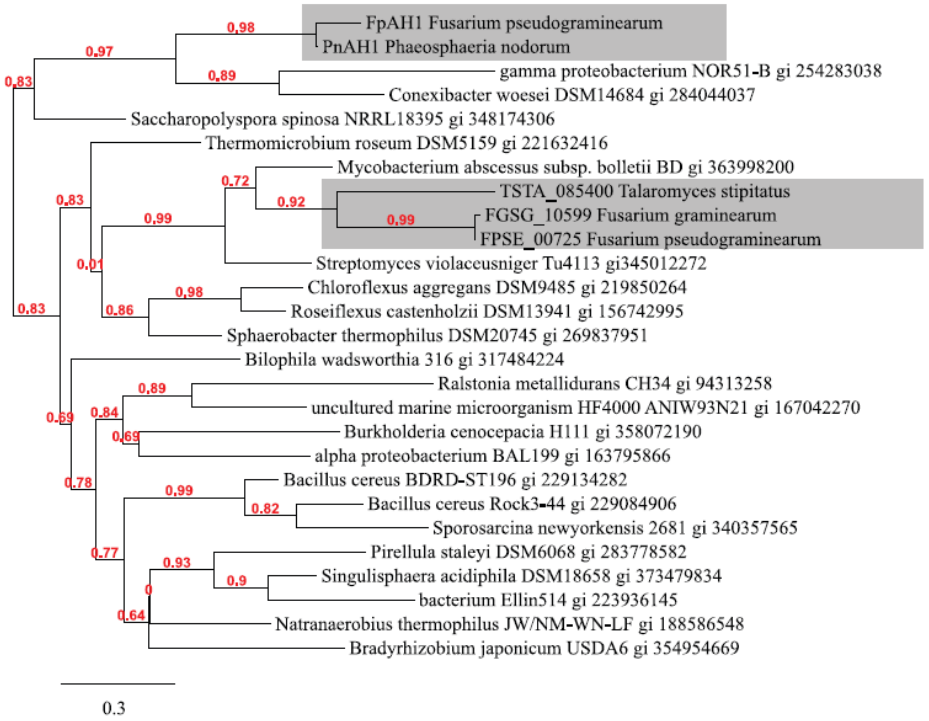


Figure 2. Phylogram of fungal amidohydrolases found in *F. pseudograminearum* that appear to be of bacterial origin and a number of bacterial amidohydrolases. Fungal sequences are highlighted in grey boxes. Numbers on branches indicate approximate likelihood ratio test branch support values.
doi:10.1371/journal.ppat.1002952.g002

Gardiner *et al.* 2012: horizontal gene transfer between fungal pathogens on wheat and barley

Interactions host-parasites

- Evolution of human/animal parasites

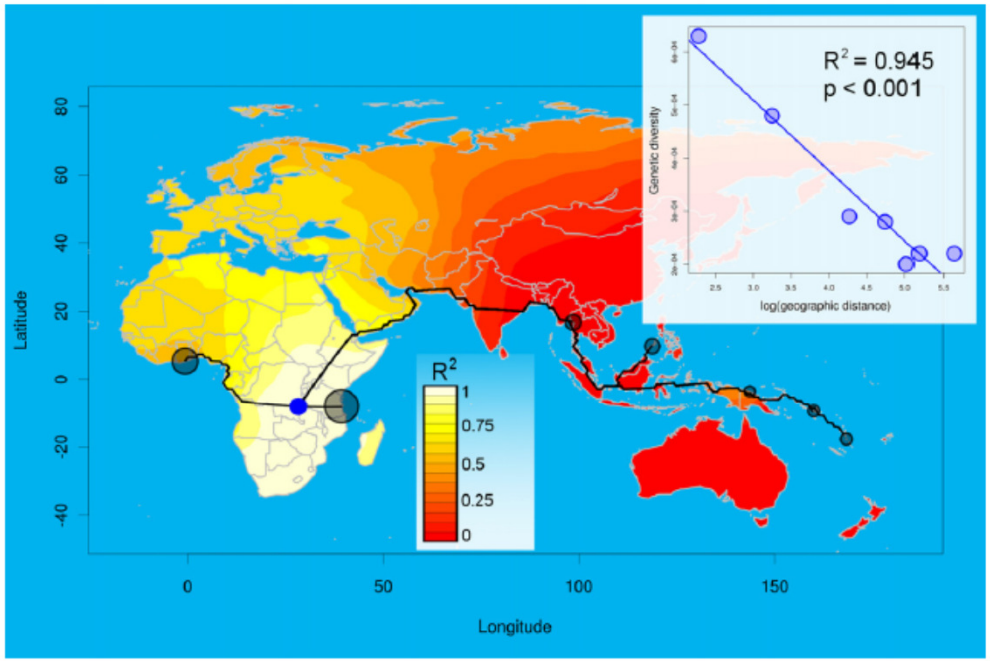
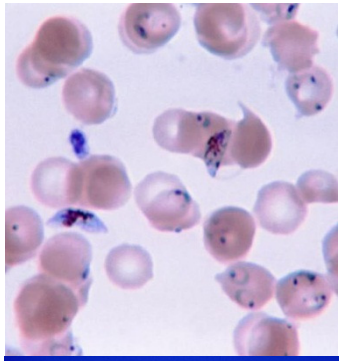


Figure 1. Map of Most Likely Origin for *Plasmodium falciparum*

Grey circles represent the geographic locations of the populations analyzed, with the surface of the circles proportional to within-population genetic diversity (θ_π). The background color represents the strength of the correlation between geographic distance from various origins and genetic diversity, with light shades representing more likely origins. The best supported origin is indicated by a blue dot. We also represented the colonization routes from this origin through landmasses to all populations analyzed (see Experimental Procedures). The inset represents the correlation between geographic distance (measured as travel cost over friction routes) and genetic diversity for the best supported origin.



Tanabe *et al.* 2010: Origin and population structure of *Plasmodium falciparum* (malaria)

Interactions host-parasites

- Evolution of human/animal parasites

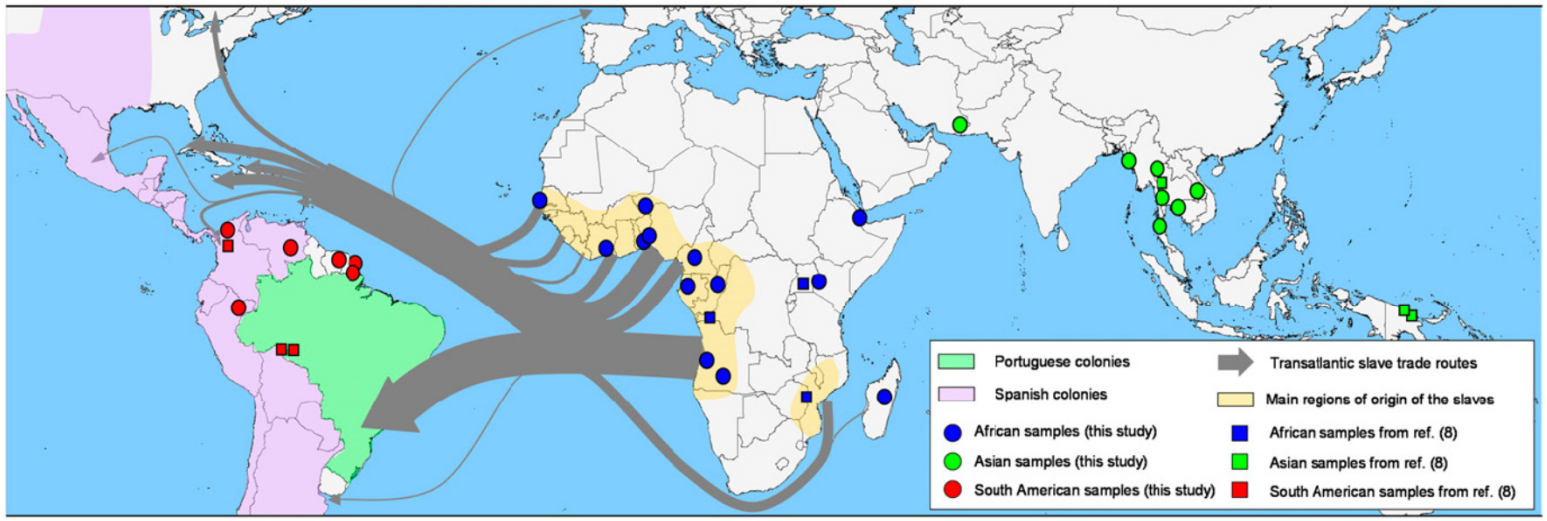


Fig. 1. Sampling sites, main routes of the transatlantic slave trade, and major European Empires between the 16th and the 19th centuries in South America. Circles represent populations sampled for this study: the MS dataset. Squares represent populations sampled in ref. 8. The MS+ dataset includes all populations. Detailed information is in *SI Appendix*, Table S1.

Yalcindag *et al.* 2012: Origin and population structure of *Plasmodium falciparum* in South-America

Proof of coevolution

What constitutes evidence for coevolution?

- three criteria (in decreasing order of stringency)
- **the selection criterion**
  - the evolution of the interaction is observed (or reciprocal trait evolution reconstructed on a phylogeny)
- **the perturbation criterion**
- an experimental perturbation leads to observable changes in the reproductive success of the partners
- **the functional criterion**
  - an interaction affects the reproductive success of both partners and is beneficial for at least one (if not, it does not occur)

- ***many classical examples of coevolution only represent 'adaptive story-telling'***
  - ***in order show convincingly that an interaction has a coevolutionary origin one must show that it has resulted from reciprocal evolutionary change***