

Fungal Diversity

Isheng Jason Tsai

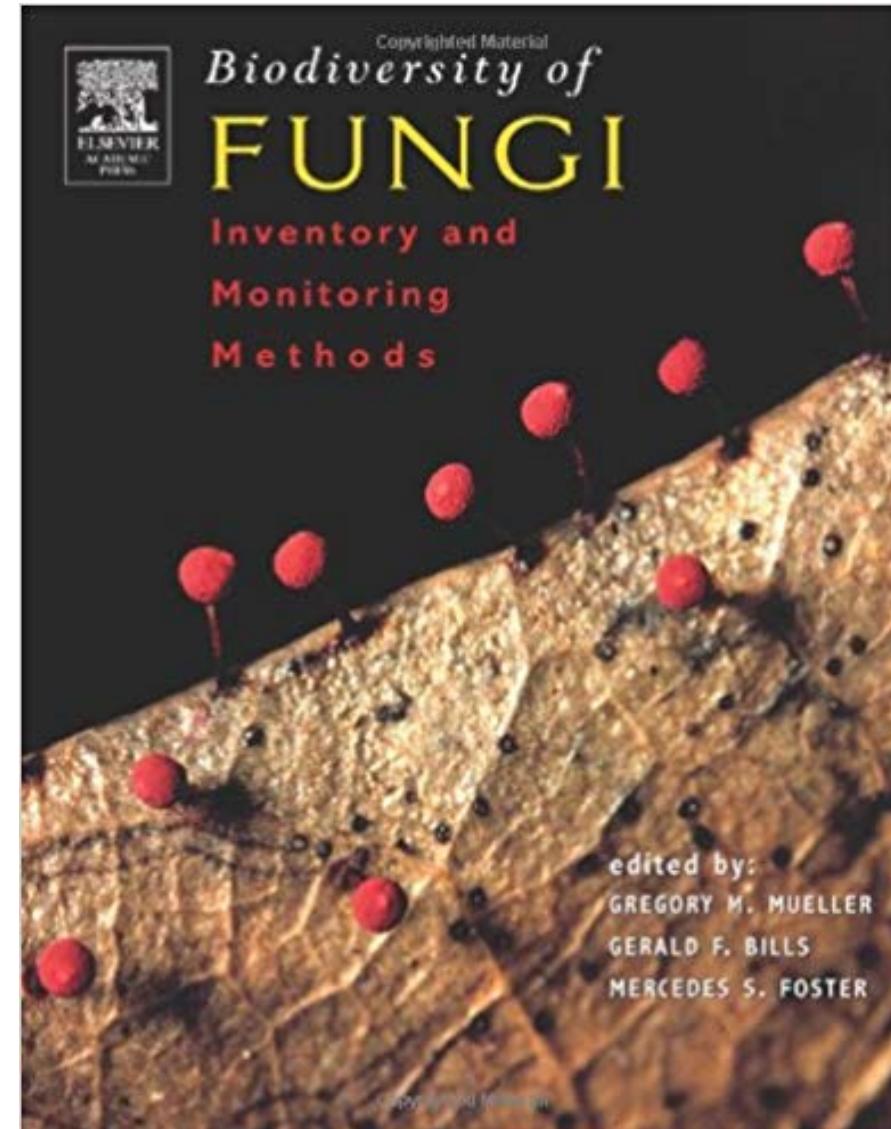
Lecture 2019.03.12



Lecture objective

- Fungal diversity – a description
- Their impact on ecology
- How do we study them? Some case studies.

Recommended text



<https://www.kew.org/state-of-the-worlds-fungi>

Video references

National Geographic - Kingdom Of The Forest - Fungi

<https://www.youtube.com/watch?v=zb4y40kFhL4>

Fungi matter

<https://youtu.be/H9KLf-URS1g>

The Wonderful World Of Fungi Documentary 2018

<https://www.youtube.comv=H9KLf-URS1g>

Lecture outline

General descriptions of fungi

The "good"

The "bad"

Methods of studying fungi

Fungal genomics

Case studies

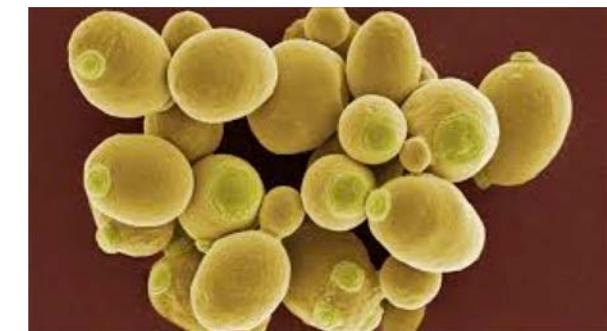
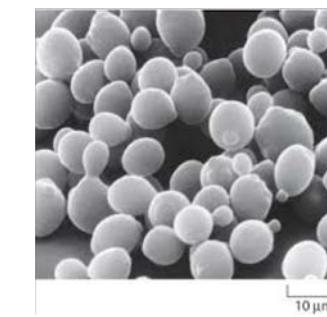
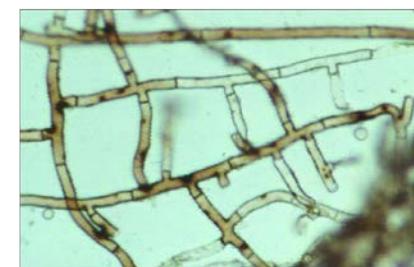
General descriptions of fungi

fungus (n.)

1520s, "a mushroom," from Latin *fungus* "a mushroom, fungus;" used in English at first as a learned alternative to *mushroom* (*funge* was used in this sense late 14c.). The Latin word is believed to be cognate with (or derived from) Greek *sphongos*, the Attic form of *spongos* "sponge" (see **sponge** (n.)). "Probably a loanword from a non-IE language, borrowed independently into Greek, Latin and Armenian in a form **sphong-*" [de Vaan]

“The concept of a “fungus” has developed over many years, and the historic definition of fungi as nonphotosynthetic plants has been shown to be both too simplistic and phylogenetically inaccurate”

Fungi are eukaryotes



2300 × 2800 - biology...

General Characteristics of Fungi

- Cell wall present, composed of cellulose and/or chitin.
- Food storage - generally in the form of lipids and glycogen.
- Eukaryotes - true nucleus and other organelles present.
- Most fungi require water and oxygen (no obligate anaerobes).
- Fungi grow in almost every habitat imaginable, as long as there is some type of organic matter present and the environment is not too extreme.
- Diverse group, number of described species is ~**70,000** (estimated 5.1 million species total).

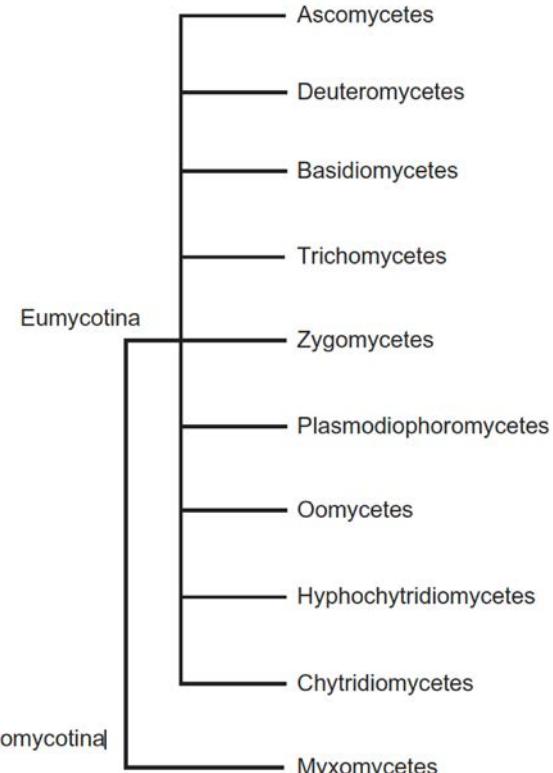
Fungal systematics – introduction

- Phyla within the fungi are defined primarily on the basis of life cycles, mode of reproduction, and cell wall and septum structure.
- One important feature of the fungi is that many have life cycles that consist of two or more stages. These are primarily differentiated by the mode of reproduction and may be asexual, where growth and reproduction is by mitosis, or sexual, where reproduction involves meiosis.
- A fungus either producing asexual diaspores or no spores at all is termed ***anamorphic*** or imperfect, and the sexual state when present is termed the ***teleomorph*** or the perfect state. The mode of **sexual reproduction** is a major characteristic for assigning individual fungi to phyla, and a fungus that is known only from its vegetative state cannot be easily placed in a phylum using traditional morphological analysis. Historically such fungi were placed in an additional phylum, the “**Deuteromycota**.” This placement, however, suggests a phylogenetic relationship between vegetative fungi that has been demonstrated to be incorrect.
- When anamorph and teleomorph forms both exist and occur separately, **there are generally dual names**, with **one name being used for the anamorph and a different name being used for the teleomorph**. In some cases, the morphology of the anamorph can be very basic, and so apparently similar anamorphic forms may produce different and sometimes unrelated teleomorphs. This occurs commonly in the Ascomycetes, and examples of common anamorphic genera with more than one genus of teleomorph include *Phoma*, *Aspergillus*, and *Paecilomyces*.

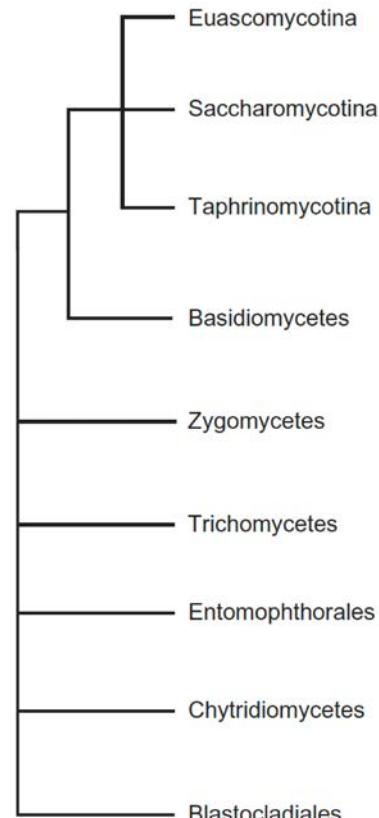
Fungal systematics – a history

- Traditional Fungal Systematics Relying on Morphological or Other Phenotypic Characters (1729–1864)
- Fungal Systematics Using Physiological and Biochemical Characters (1865–1989)
- Fungal Phylogeny Based on One or a Few Genes (1990–2005)
- **Fungal Phylogenomic Analysis (2006–Present)**

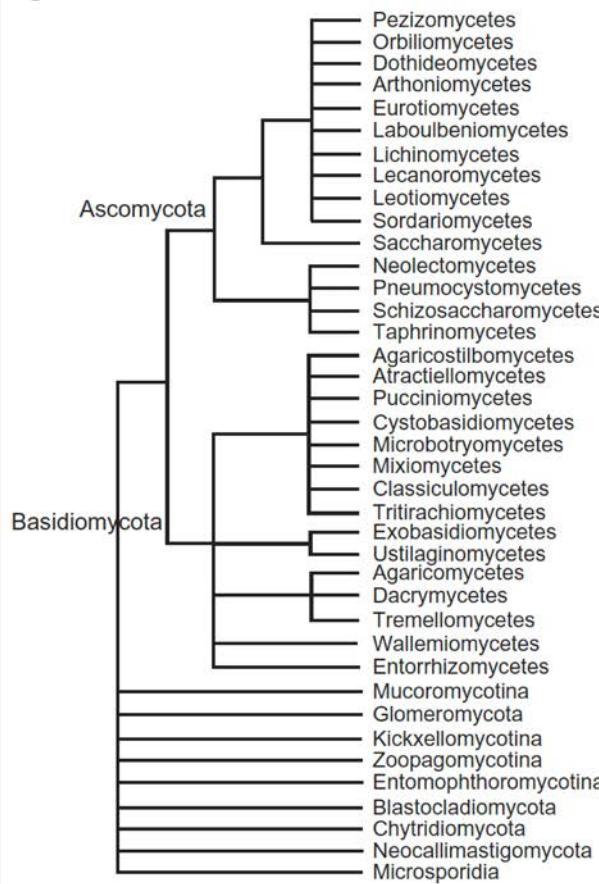
A



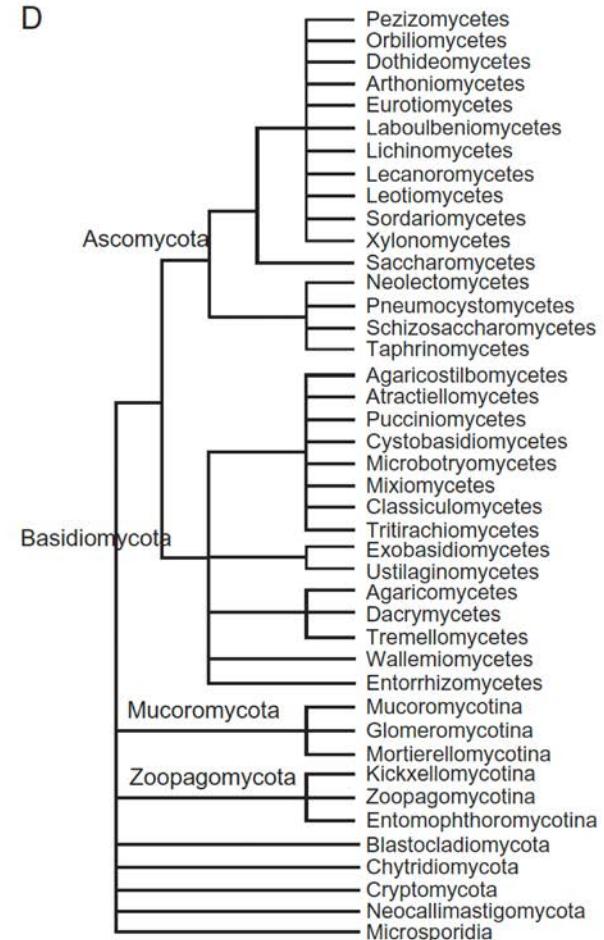
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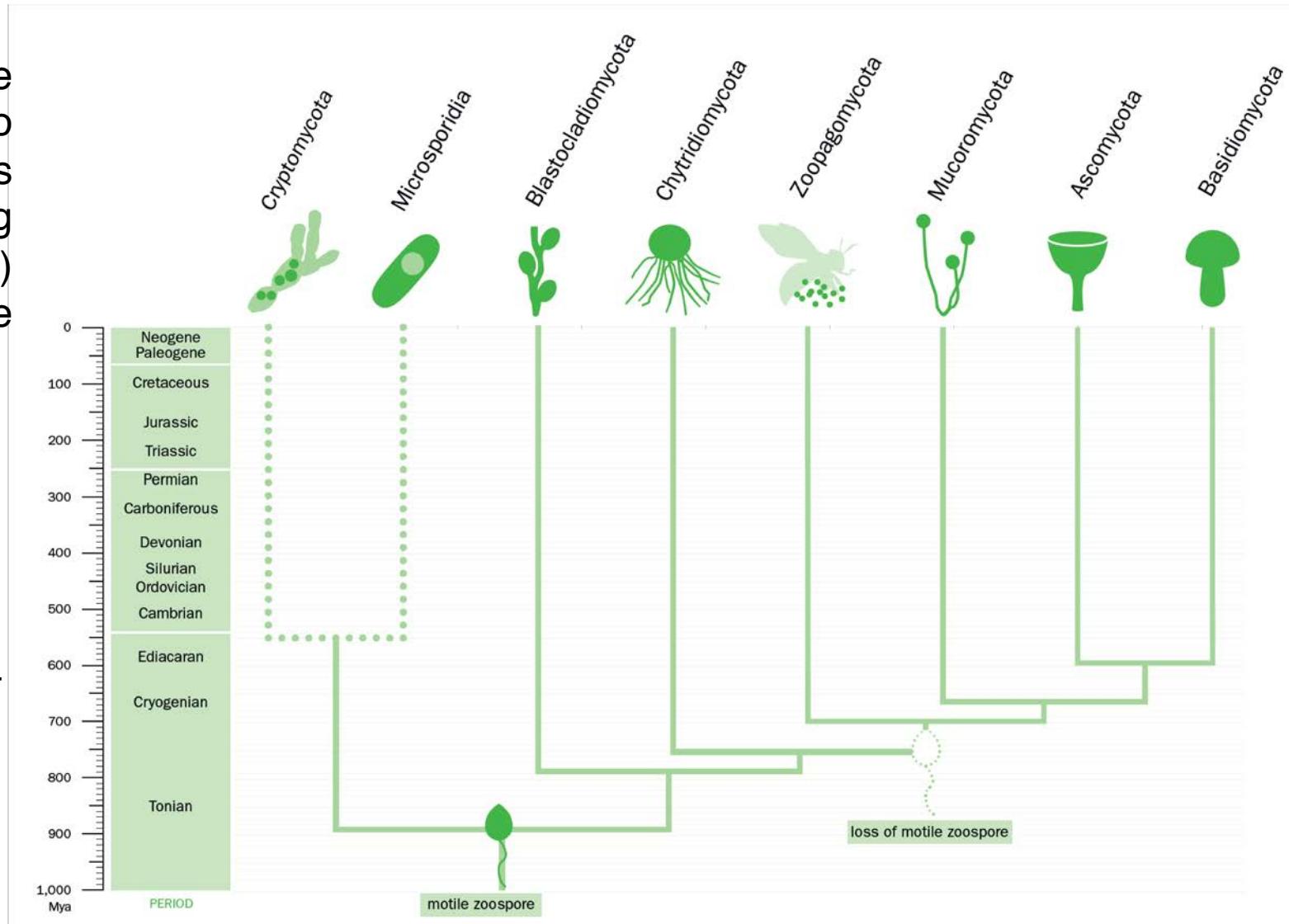
D



Fungi phylogeny

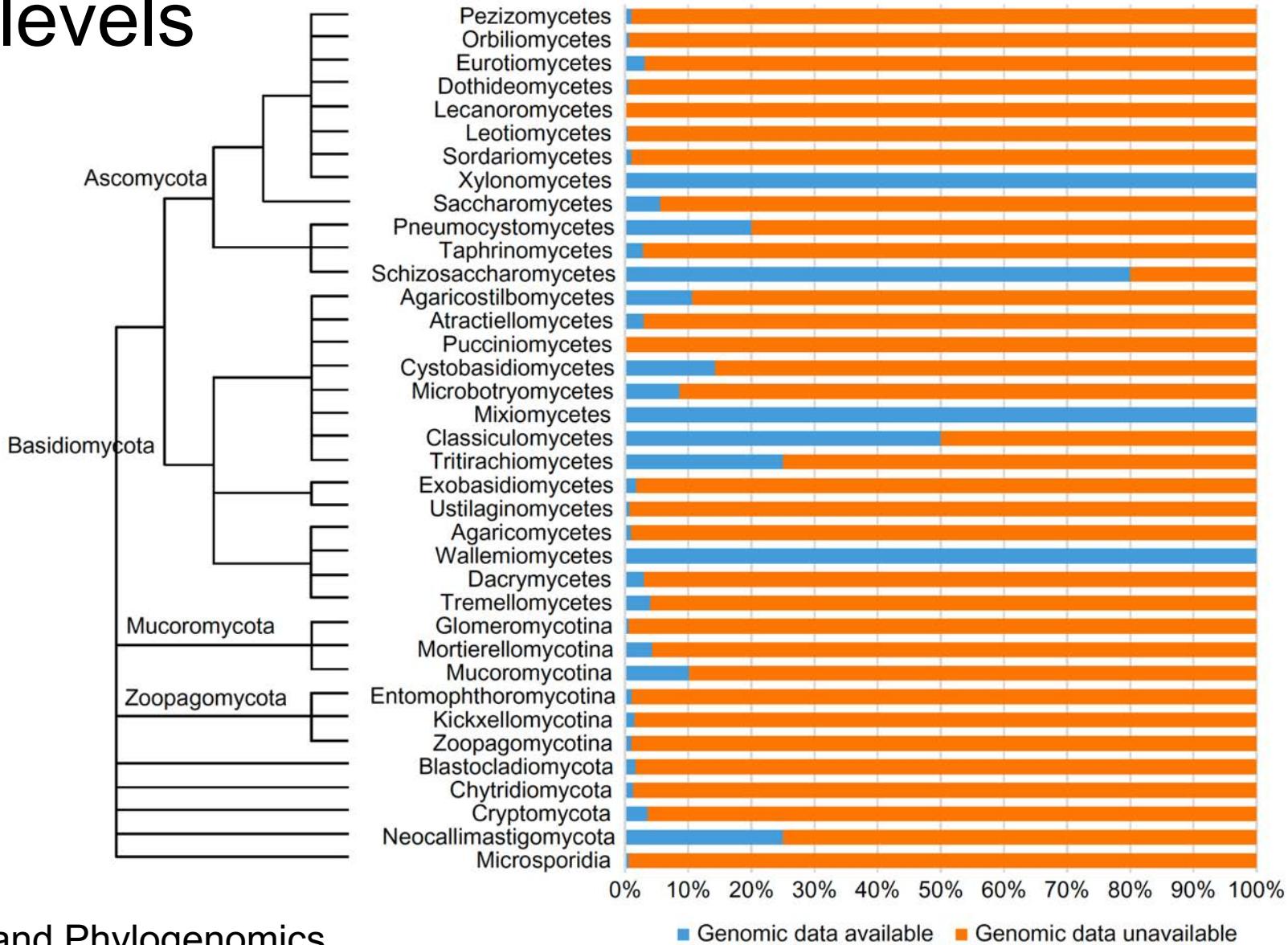
The earliest fungi are thought to have evolved around **1 billion years ago** and to have been simple, single-celled organisms living in water and reproducing using motile asexual spores (zoospores) propelled by a posterior whip-like structure called the flagellum

The evolution of the two fungal groups that contain species capable of forming highly complex spore-bearing structures (i.e. Ascomycota and Basidiomycota) is considered to have occurred around 600–700 Mya. Together they contain the vast majority of known fungal species diversity – **c. 90,000 species in Ascomycota and c. 50,000 species in Basidiomycota**

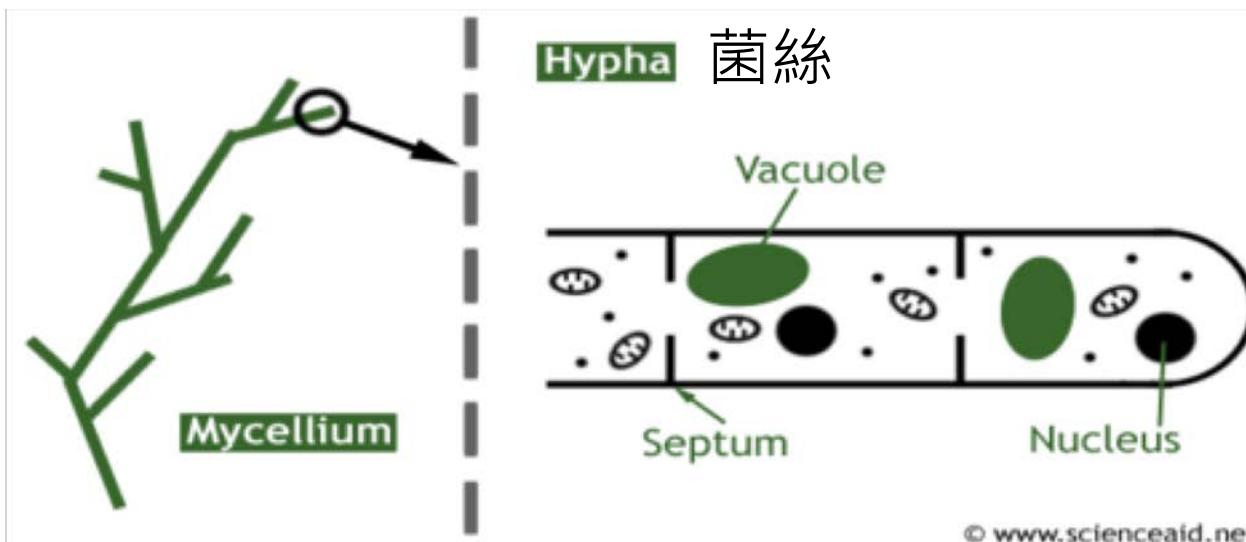


Relative proportion of fungal taxa with released genomes among published taxa at the class or higher levels

- Despite advances in phylogenomics, many fungal groups are still woefully undersampled
- A final note of caution needs to be made about horizontal gene transfer (HGT), the bane of multigene phylogenetics



Fungi structure

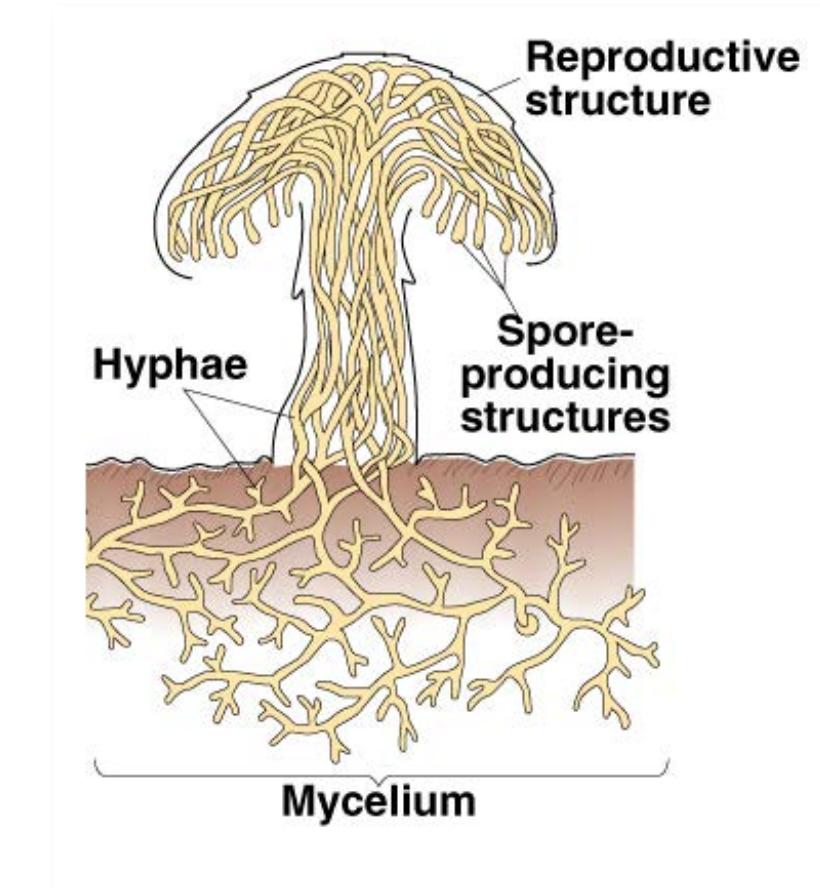


sclerotium = hardened mass of mycelium that generally serves as an overwintering stage.
multicellular, such as mycelial cords, rhizomorphs, and fruit bodies (mushrooms)

Body form

unicellular filamentous (tube-like strands called hypha (singular) or **hyphae** (plural))

mycelium = aggregate of hyphae



Fungi are heterotrophs ('other food')

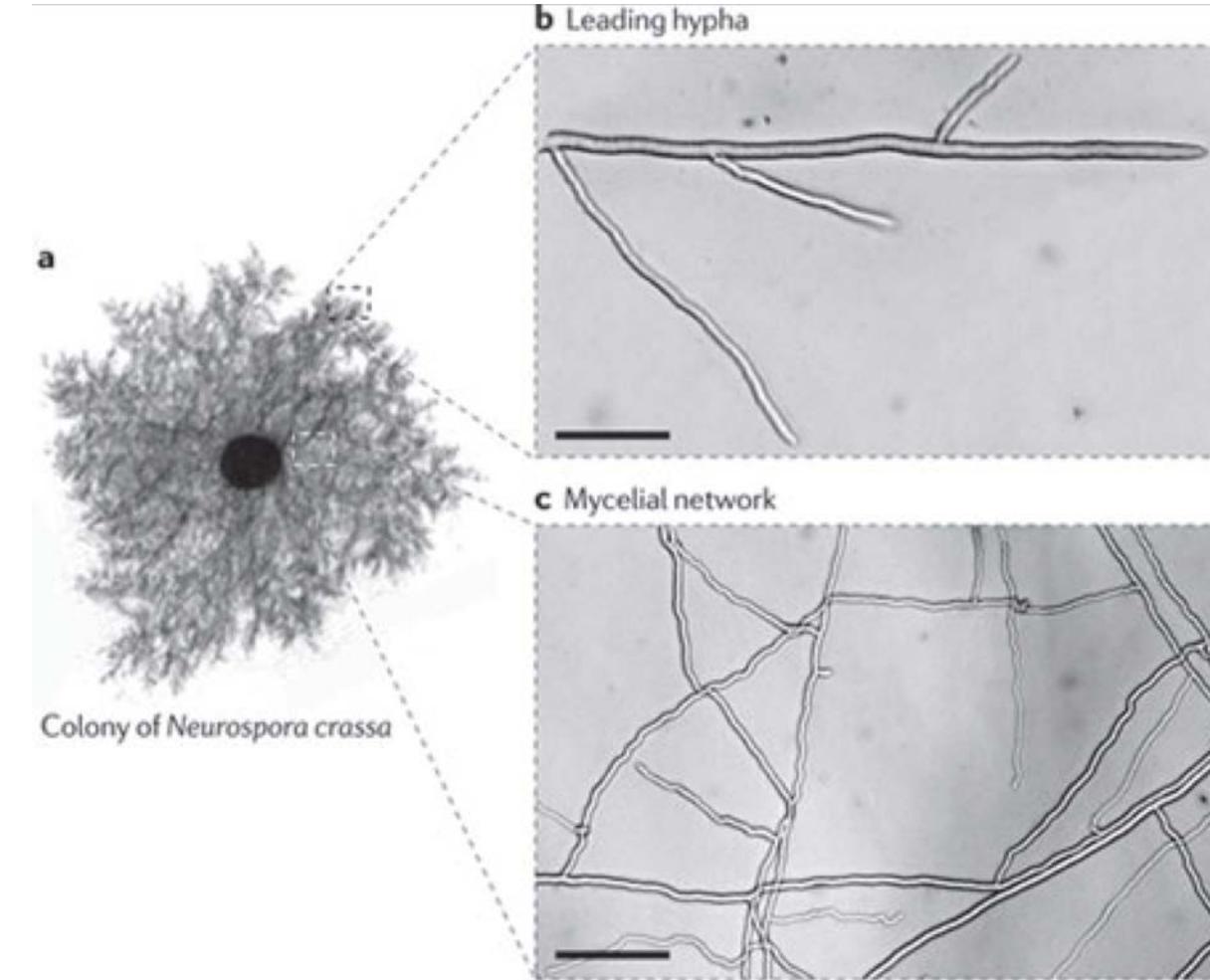
- i.e., acquire nutrients by absorption



Credit: UWA 2005

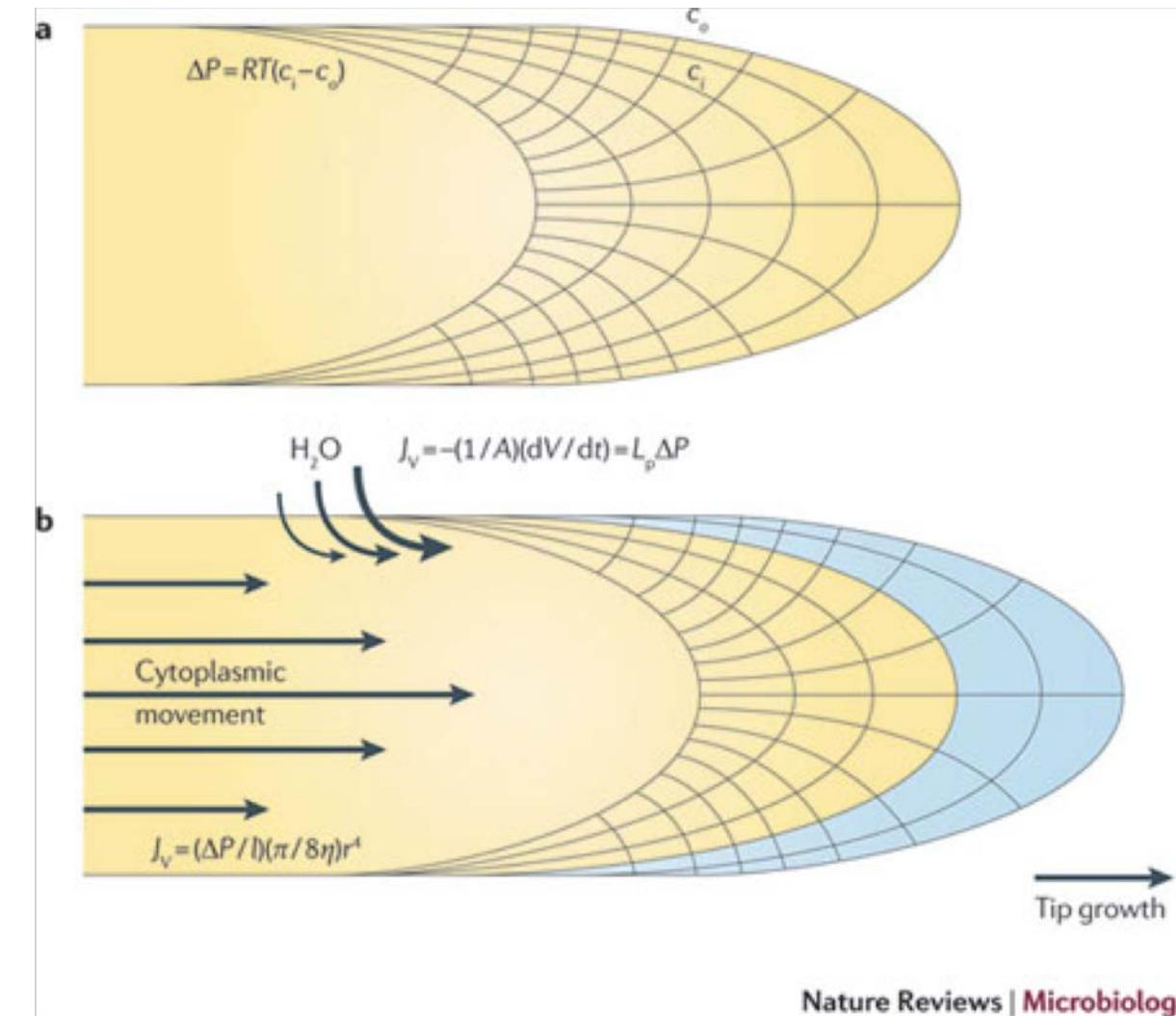
- Three main types:
 - **Saprophytes** or saprobes - absorb nutrients from dead organic material
 - **Parasitic** fungi - absorb nutrients from cells of living hosts; some are pathogenic
 - **Mutualistic** fungi - absorb nutrients from a host, but reciprocate to benefit the host

Hyphal growth



Nature Reviews | Microbiology

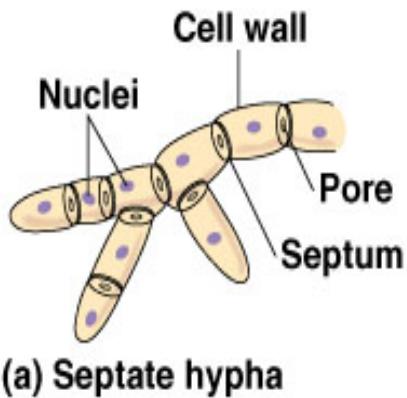
is of the order of 5–10 μm in diameter, and their immediate effect on the environment is restricted to a few micrometers on each side of these hyphae



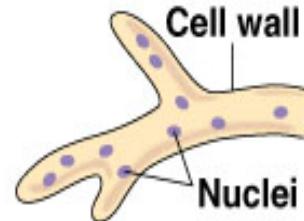
Nature Reviews | Microbiology

Lew et al., (2011)

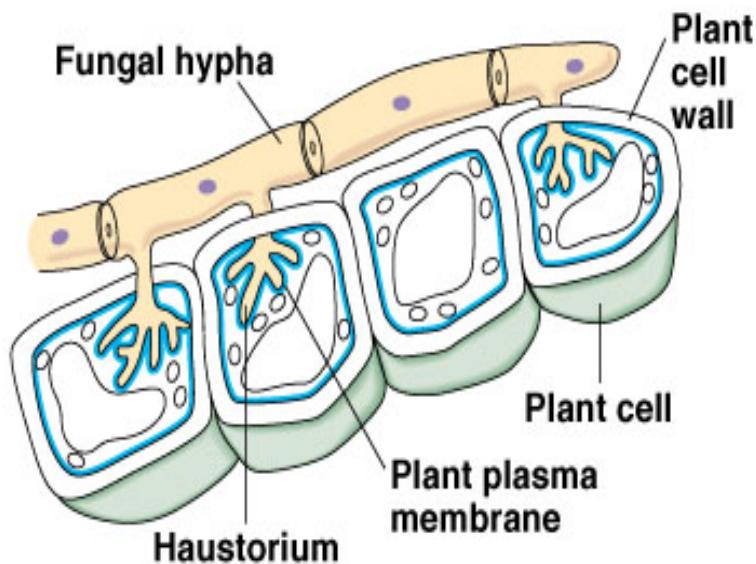
Hyphae modifications



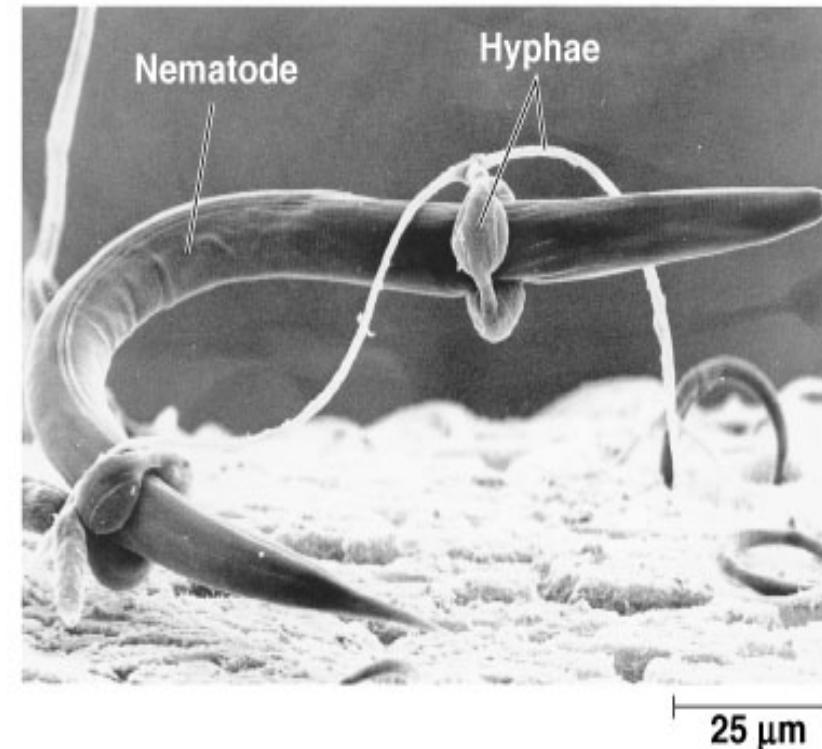
(a) Septate hypha



(b) Coenocytic hypha



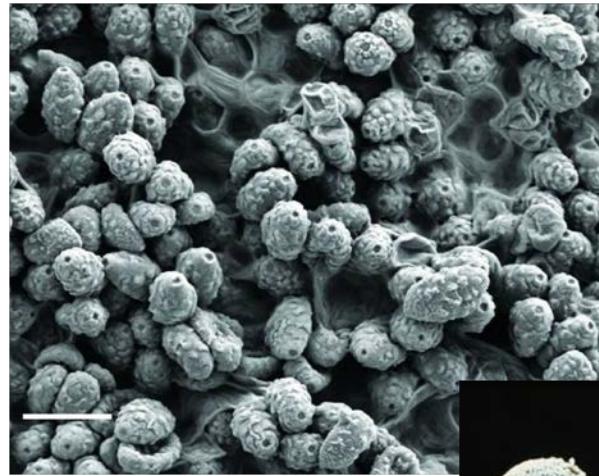
(c) Haustoria



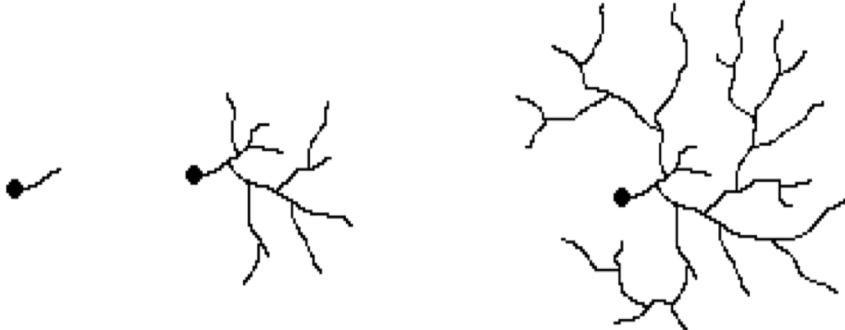
(d) Hyphae adapted for trapping and killing prey

Spores 胞子

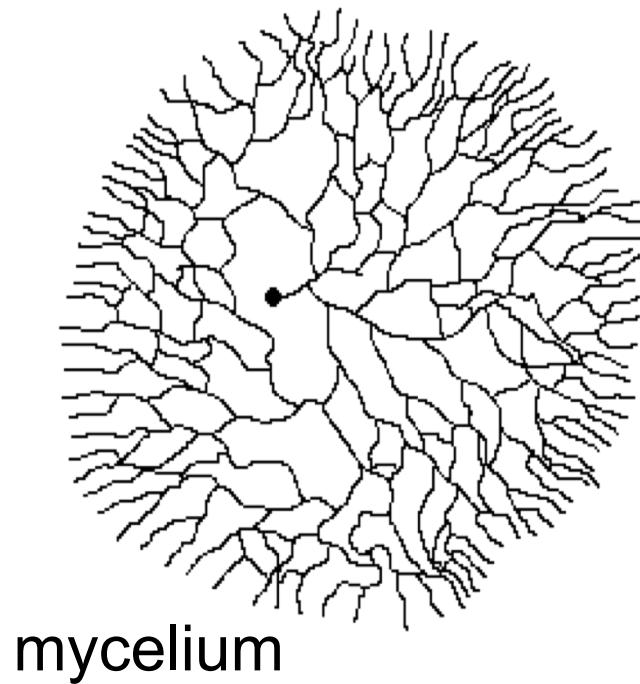
- Spores can arise both from sex (harsh condition?) or asexual (favourable condition?) phases
- Purpose of Spores
 - Allows the fungus to move to new food source.
 - Resistant stage - allows fungus to survive periods of adversity.
 - Means of introducing new genetic combinations into a population
- Formed:
 - Directly on hyphae
 - Inside sporangia
 - Fruiting bodies



Hyphal growth from spore



germinating spore



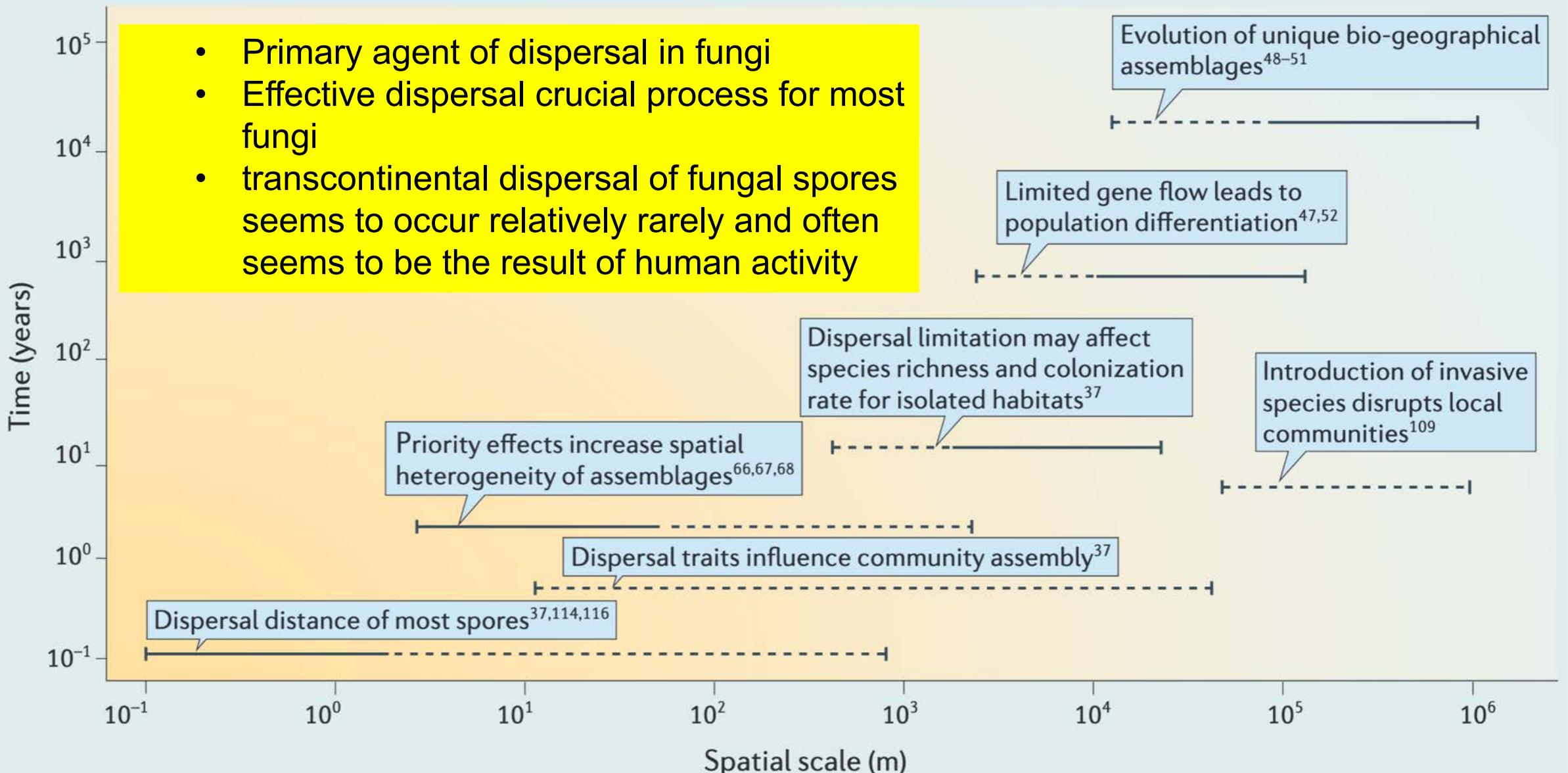
mycelium



▲ FIGURE 60

Is this the largest organism in the world? This 2,400-acre site in eastern Oregon had a contiguous growth of mycelium before logging roads cut through it. Estimated at 1,665 football fields in size and 2,200 years old, this one fungus has killed the forest above it several times over, and in so doing it has built deeper soil layers that allow the growth of ever-larger stands of trees. Mushroom-forming forest fungi are unique in that their mycelial mats can achieve such massive proportions.

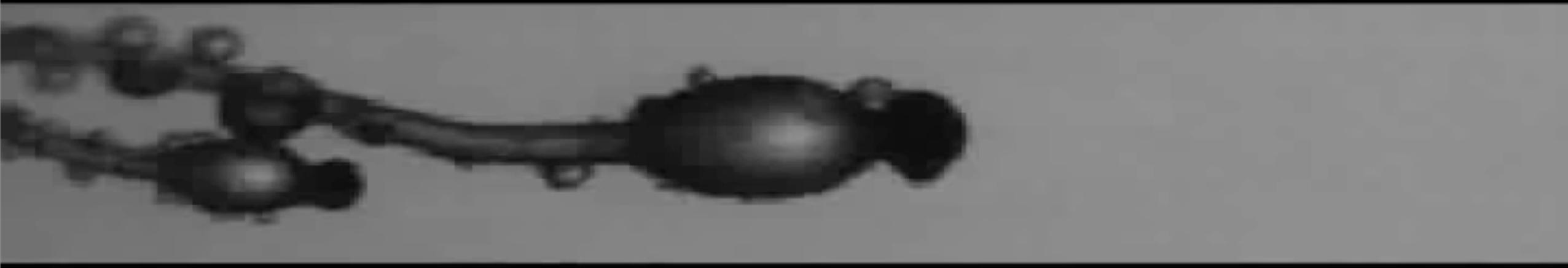
Spore dispersal



Fungi are everywhere



Photo credit: 張道弘



Rifle acceleration = 9,395G

Shotgun acceleration = 9,313G

Pilobolus acceleration = 20000G!!!!

Division Ascomycota 子囊菌门

: sac fungi produce sexual spores in saclike ascospores

Sexual Reproduction – ascospores (sing. = ascus)

Asexual reproduction is common

Cup fungi, morels, truffles

Important plant parasites & saprobes

Yeast - *Saccharomyces*

Decomposers, pathogens, and found in
most lichens



A cluster of ascospores with spores inside

Basidiomycota – “club fungi”

- Named after transient diploid stage: basidium
- Important decomposers of wood / plant material
- Include:
 - Mycorrhiza-forming mutualists
 - Mushroom-forming fungi
 - Plant parasites e.g. rusts and smuts
- Characterised by dikaryotic mycelium that reproduces sexually via basidiocarps
- Sexual Reproduction – basidia
- Asexual reprod – not so common
- Long-lived **dikaryotic** mycelia
- Rusts & smuts –plant parasites
- Mushrooms, polypores, puffballs, boletes, bird's nest fungi
- Enzymes decompose wood, leaves, and other organic materials
- Decomposers, pathogens, and some form mycorrhizal associations with plants

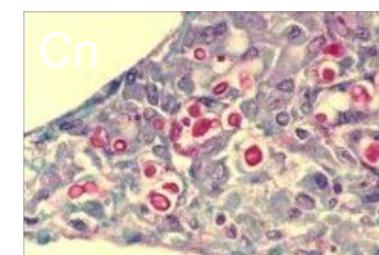
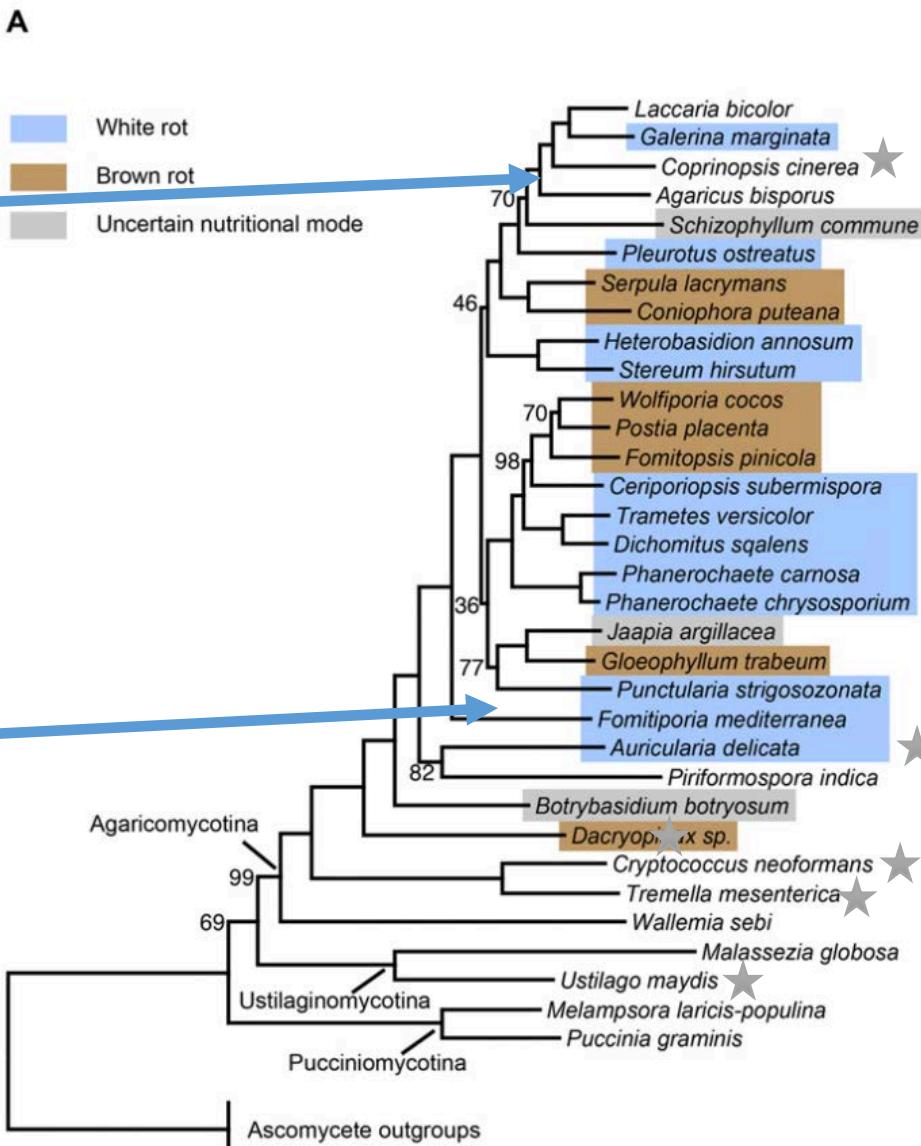
Phylogeny of basidiomycetes 擔子菌綱



Mycena



Phellinus noxius

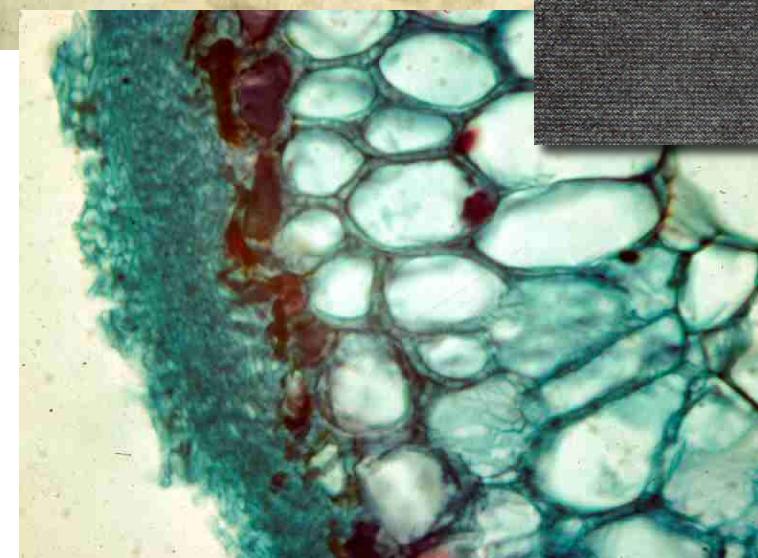
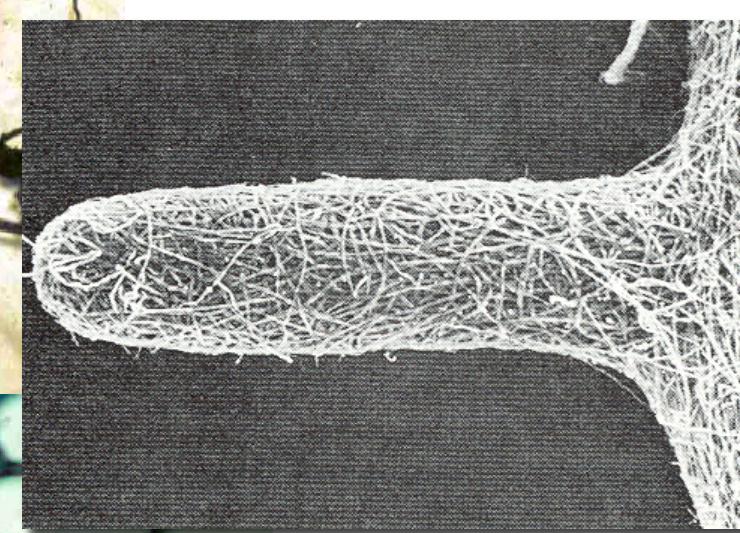


Mycorrhizae 菌根

- “Fungus roots”
- Mutualism between:
 - Fungus (nutrient & water uptake for plant)
 - Plant (carbohydrate for fungus)
- Several kinds
 - Zygomycota – hyphae invade root cells
 - Ascomycota & Basidiomycota – hyphae invade root but don’t penetrate cells
- Extremely important ecological role of fungi!



Russula
mushroom
mycorrhizas on
Western
Hemlock root



Main types of Mycorrhizae and their plant partners

MYCORRHIZAL TYPE	PLANT PARTNER	FUNGAL PARTNER	MAIN ECOSYSTEMS
Ectomycorrhizal fungi	2.2% of plant species, especially woody species; Pinaceae (e.g. pine, spruce, fir, larch) and angiosperms (e.g. beech, oak, chestnut, hazelnut, rockrose)	20,000 Basidiomycota and Ascomycota species	Temperate, boreal, mediterranean, and some tropical forests
Arbuscular mycorrhizal fungi	78% of plant species; Herbs, shrubs, trees, liverworts, hornworts, lycopods and ferns	300–1,600 Mucoromycota (Glomeromycotina) species	Tropical and temperate forests, grasslands, savannas, shrublands, deserts, agricultural crops
Ericoid mycorrhizal fungi	1.5% of plant species; Ericaceae (e.g. heather, rhododendron, blueberry) and liverworts	>150 Ascomycota and some Basidiomycota species	Heathlands, tundra, boreal and temperate forests
Orchid mycorrhizal fungi	10% of plant species; Orchidaceae (orchids)	25,000 Basidiomycota and some Ascomycota species	Tropical, temperate, mediterranean

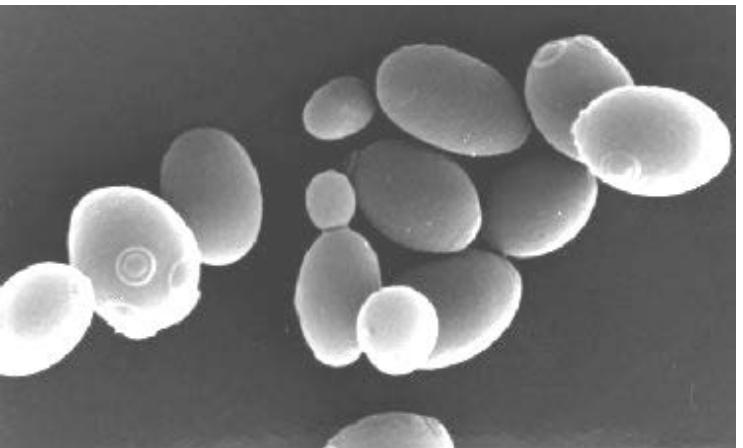
Lichens 地衣

- “Mutualism” between
 - Fungus – structure
 - Alga or cyanobacterium – provides food
- Three main types of lichens:
 - **Crustose lichens** form flat crusty plates.
 - **Foliose lichens** are leafy in appearance, although lobed or branched structures are not true leaves.
 - **Fruticose lichens** are even more finely branched and may hang down like beards from branches or grow up from the ground like tiny shrubs.

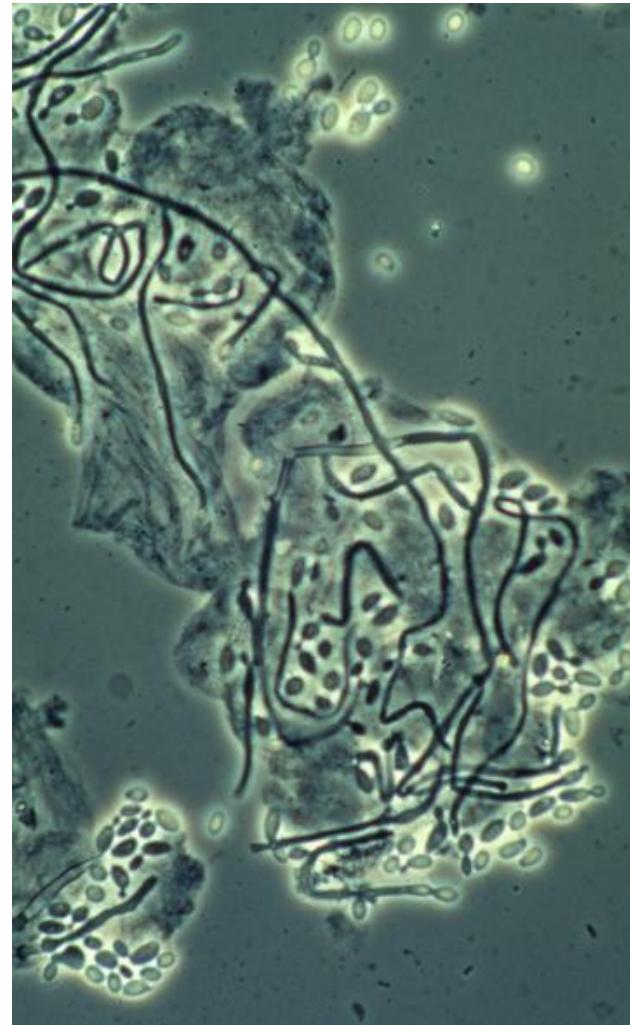


Yeasts 酵母菌

- Single celled fungi
- Adapted to liquids
 - Plant saps
 - Water films
 - Moist animal tissues



Saccharomyces



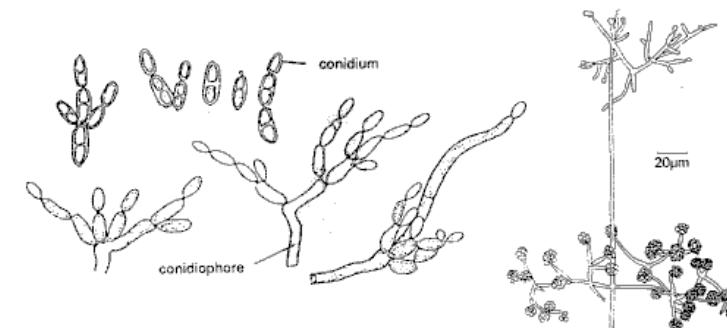
Candida

Molds 黴菌

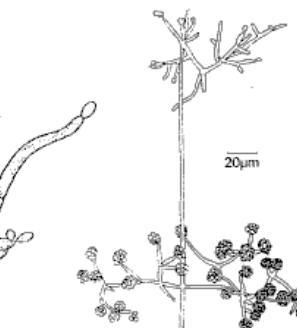
- Rapidly growth ; mostly asexual spores
- May develop into a sexual fungus, producing zygosporangia, ascocarps or basidiocarps
- Many human importances
 - Food spoilage
 - Food products (cheese flavour)
 - Antibiotics (*Penicillium*) etc.



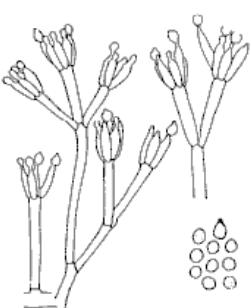
Noble Rot - *Botrytis*



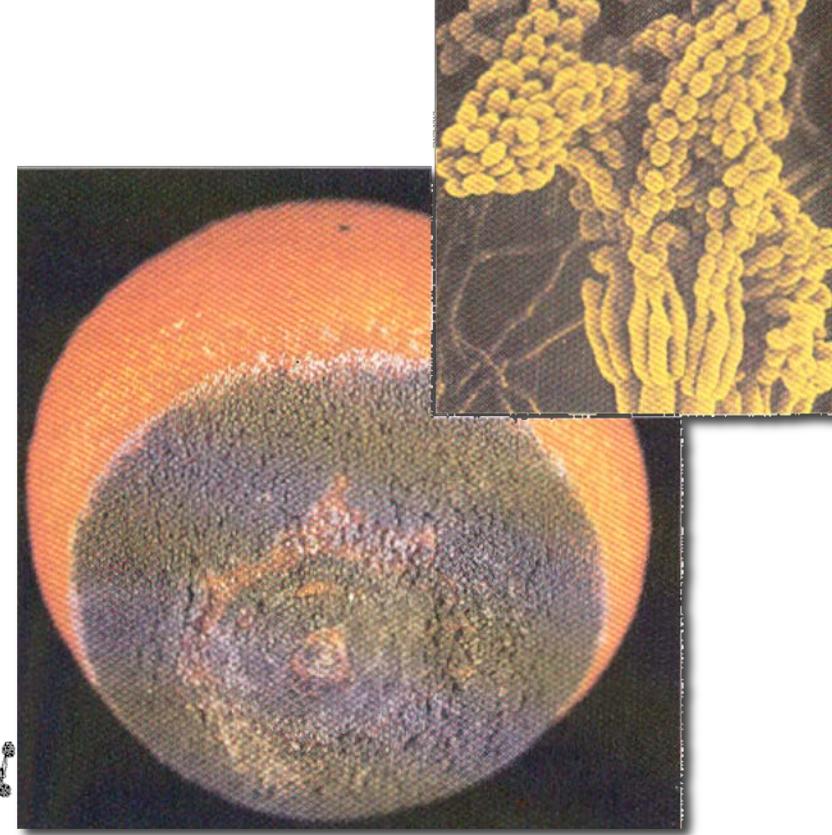
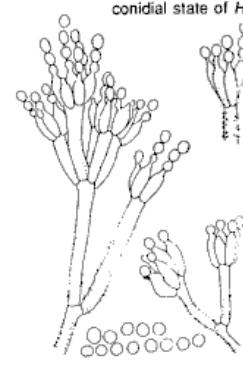
Cladosporium herbarum



Trichoderma viride
conidial state of *Hypocrea rufa*

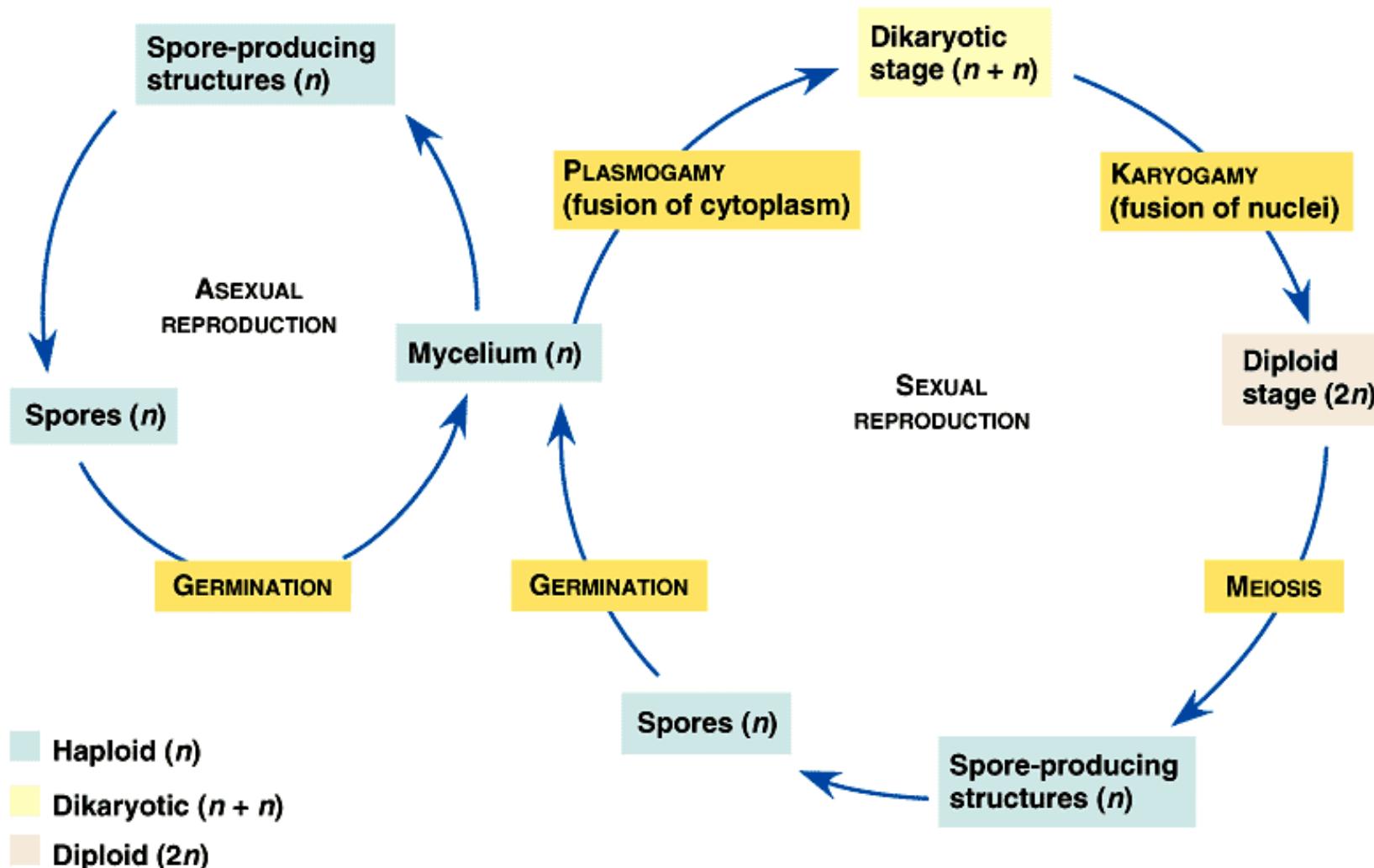


Penicillium janthinellum Conidiophores with phialospores (1000 : 1)
(a) strain with smooth-walled conidiophores; (b) strain with verrucose conidiophores with dense
branching

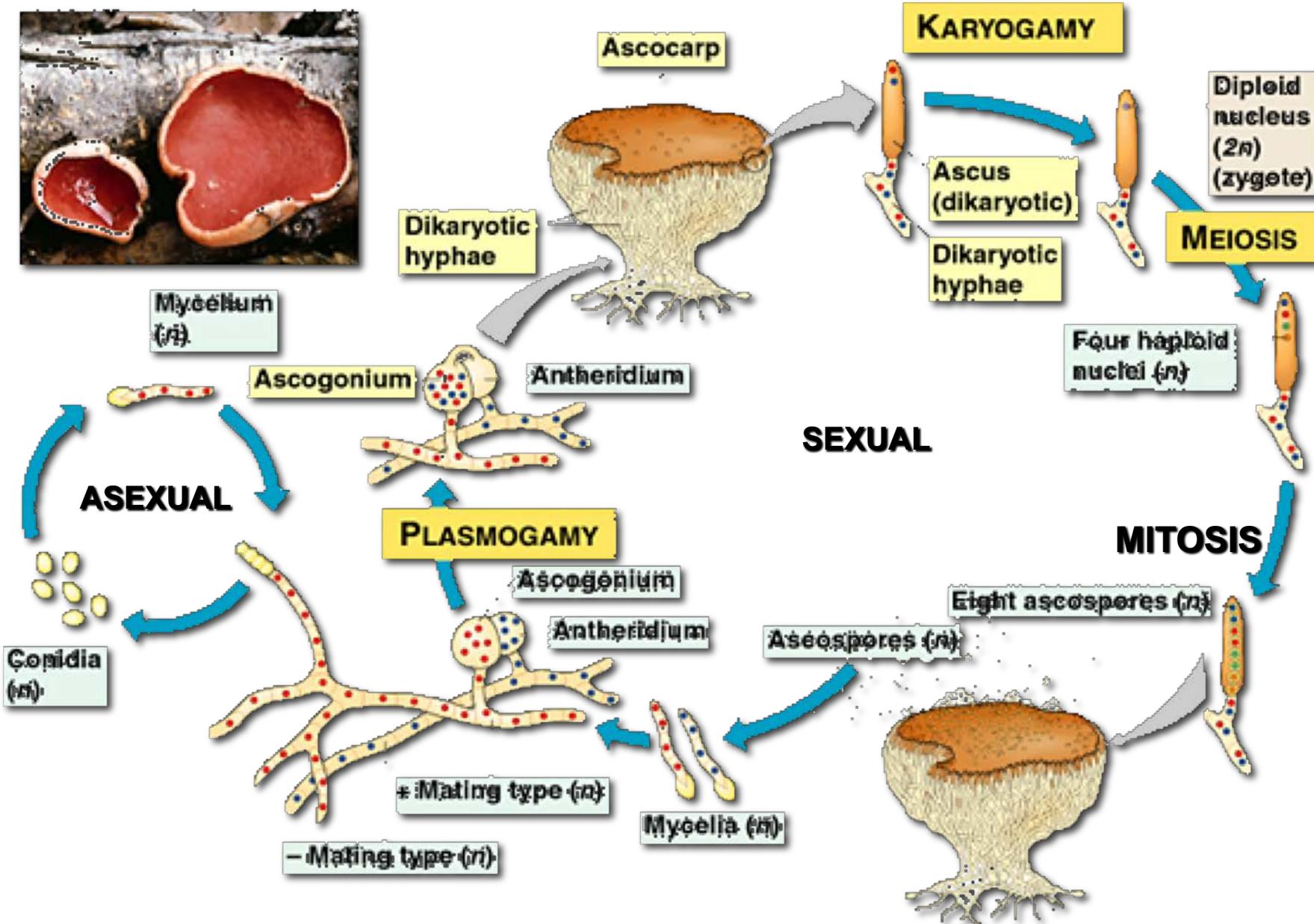


Fungal life cycle

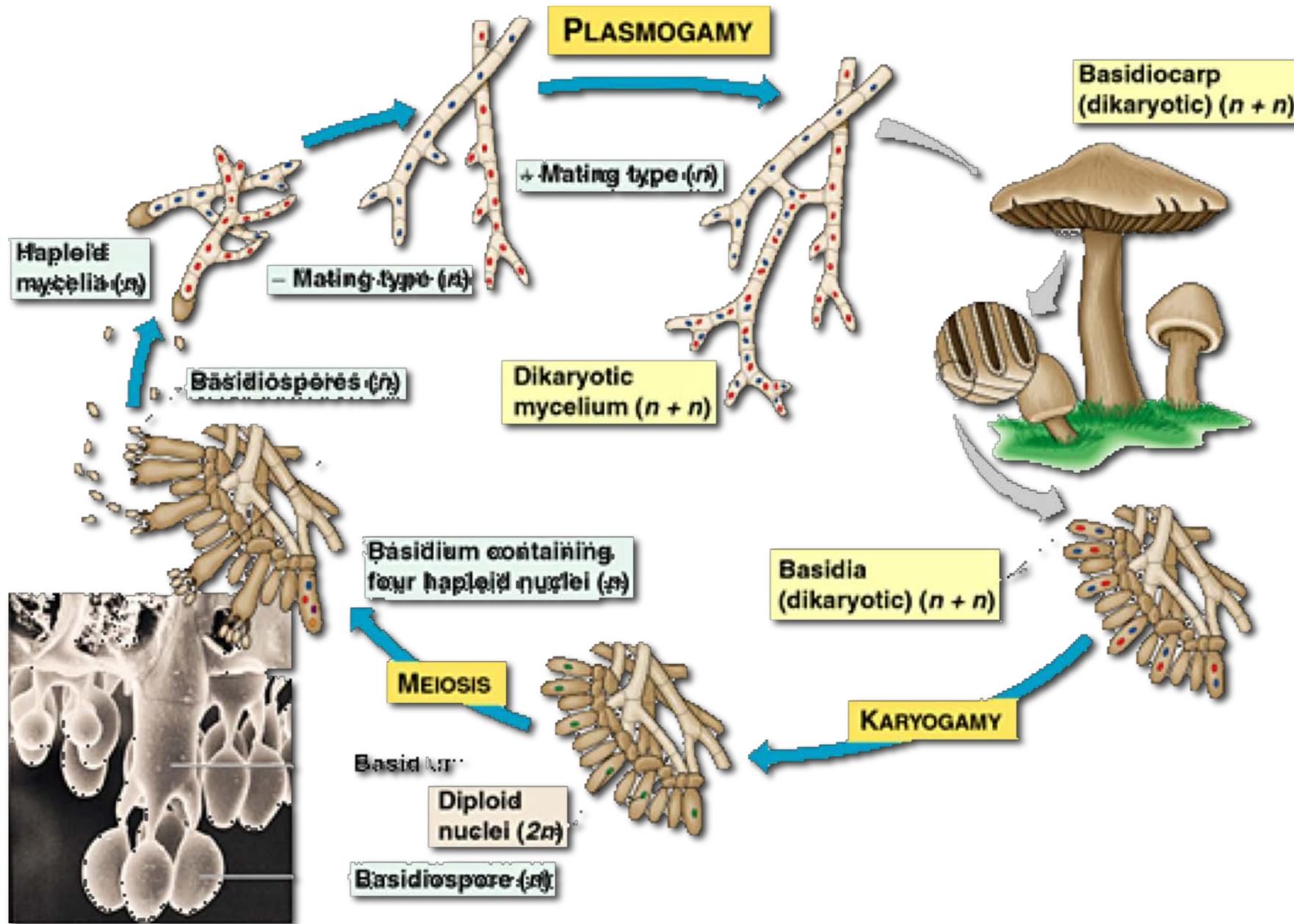
Generalized Life Cycle of a Fungus



Life cycle of an ascomycete



Life cycle of a mushroom-forming basidiomycete



Life cycle of a mushroom-forming basidiomycete

Haploid basidiospores grow into short-lived haploid mycelia: under certain conditions, plasmogamy occurs

Resulting dikaryotic mycelium grows forming mycorrhiza or mushrooms (basidiocarps)

Mushroom cap supports and protects gills: karyogamy in the terminal, dikaryotic cells lining the gills produces diploid basidia

Resulting basidium immediately undergoes meiosis producing four haploid basidiospores

Asexual reproduction less common than in ascomycetes

Fungal life style

Fungi as Symbionts (Mutualism)



PNAS



Small genome of the fungus *Escovopsis weberi*, a specialized disease agent of ant agriculture

Tom J. B. de Man^a, Jason E. Stajich^b, Christian P. Kubicek^c, Clotilde Teiling^d, Komal Chenthamara^c, Lea Atanasova^c, Irina S. Druzhinina^c, Natasha Levenkova^d, Stephanie S. L. Birnbaum^a, Seth M. Baribeau^{a,e}, Brooke A. Bozick^a, Garret Suen^f, Cameron R. Currie^f, and Nicole M. Gerardo^{a,f}

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Edited by Nancy A. Moran, University of Texas, Austin, TX, and approved February 9, 2016 (received for review September 23, 2015)

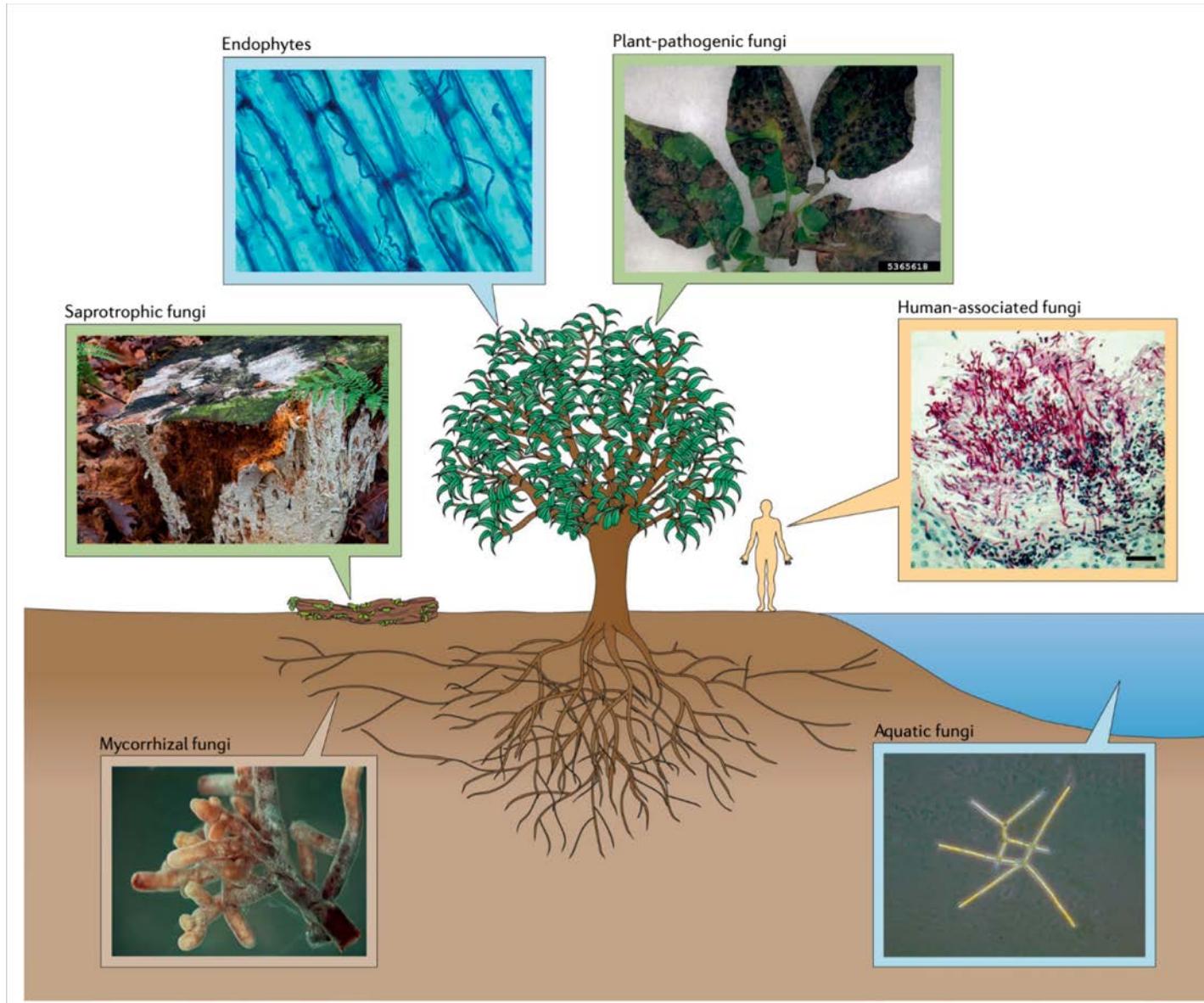
Fungi as Parasites & Pathogens



Photo by V. Jedlicka



Fungal diversity in different environments



Ecological impacts of fungi

- **Beneficial Effects of Fungi**

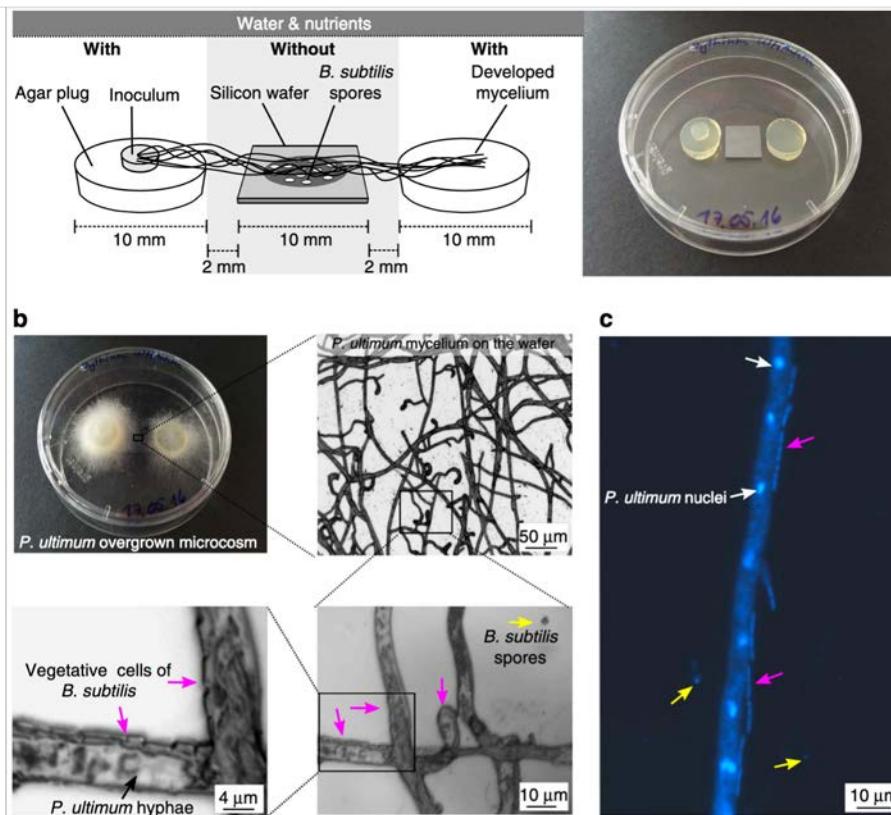
- Many organisms depend on/utilise fungi
- Decomposition - nutrient and carbon recycling.
- Biosynthetic factories. Can be used to produce drugs, antibiotics, alcohol, acids, food (e.g., fermented products, mushrooms).
- Traffic network for microorganisms and host
- Model organisms for biochemical and genetic studies.

- **(Host) Harmful Effects of Fungi**

- Destruction of food, lumber, paper, and cloth.
- Animal and human diseases, including allergies.
- Toxins produced by poisonous mushrooms and within food (e.g., grain, cheese, etc.).
- Plant diseases.

Mycelium-mediated transfer of water and nutrients stimulates bacterial activity in dry and oligotrophic environments

Anja Worrlich^{1,2,†}, Hryhoriy Stryhanyuk³, Niculina Musat³, Sara König^{2,4}, Thomas Banitz⁴, Florian Centler², Karin Frank^{4,5,6}, Martin Thullner², Hauke Harms^{2,5}, Hans-Hermann Richnow³, Anja Miltner¹, Matthias Kästner^{1,*} & Lukas Y. Wick^{2,*}



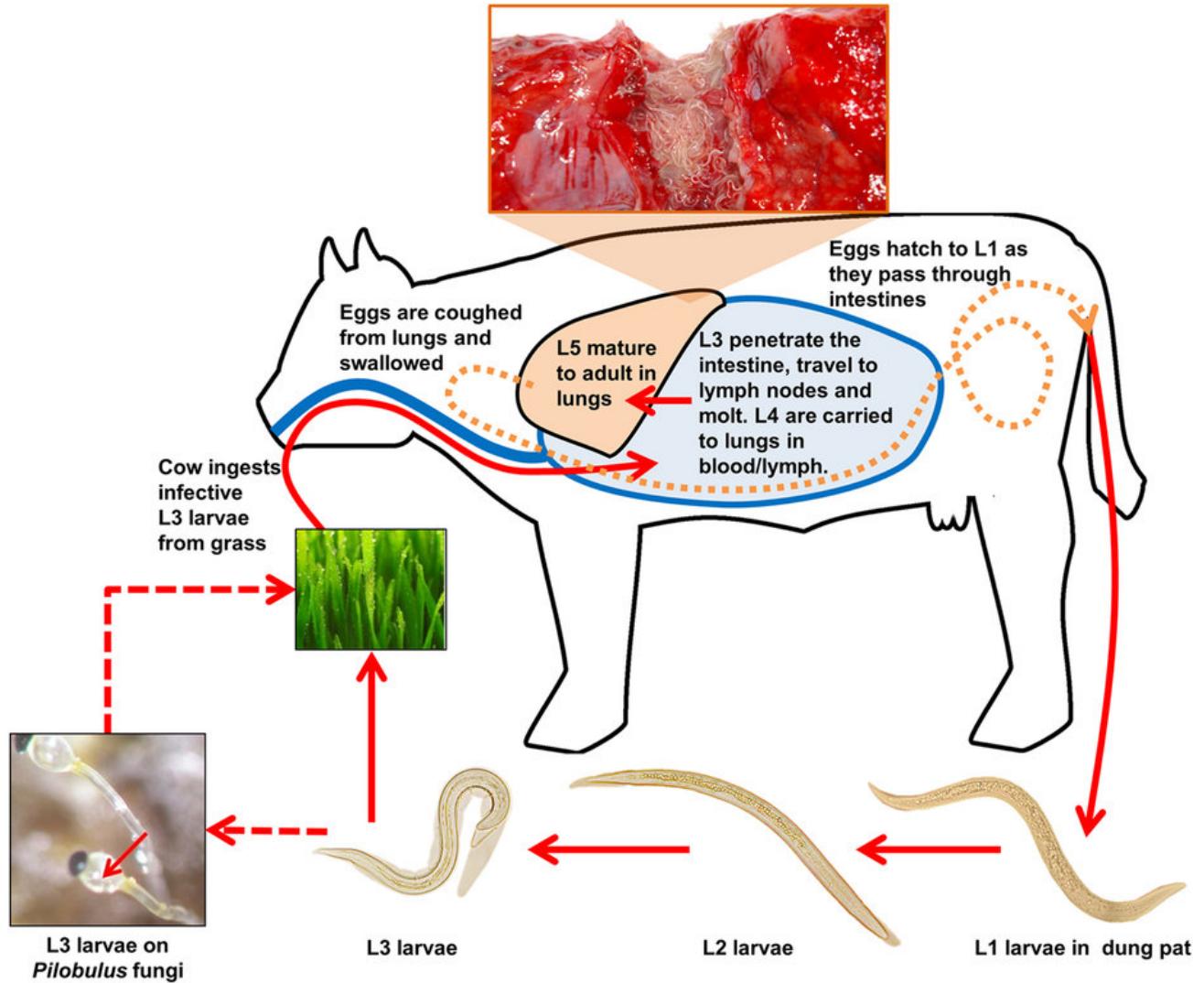
<https://www.youtube.com/watch?v=AnsYh6511lc>

Figure 1 | Synthetic microbial ecosystem reveals spore germination in presence of mycelia in dry and oligotrophic environments. (a) Scheme and photographs of the setup employed to carry out the germination, growth and labelling experiments. The synthetic ecosystem is comprised of two agar plugs serving as water and nutrient sources ('with') for the fungi or the oomycete inoculated on top of one of the agar plugs. A silicon wafer free of water and nutrients ('without') placed in the middle between the two 'with' zones served as carrier for spores of *B. subtilis*. An air gap between the 'with' and 'without' zone prevented the diffusion of water or substrates to the spore region. (b) Gradual enlargement of bright-field micrographs of the silicon wafer overgrown by mycelium of *P. ultimum*. In close vicinity to the hyphae (black arrow) rod-shaped, vegetative bacterial cells (magenta arrows) were found, whereas smaller, round-shaped spores (yellow arrows) were located more distantly. (c) Fluorescence micrograph of the 4',6-diamidino-2-phenylindole (DAPI)-stained wafer showing *P. ultimum* hyphae containing nuclei (white arrows) and vegetative cells as well as spores of *B. subtilis*.

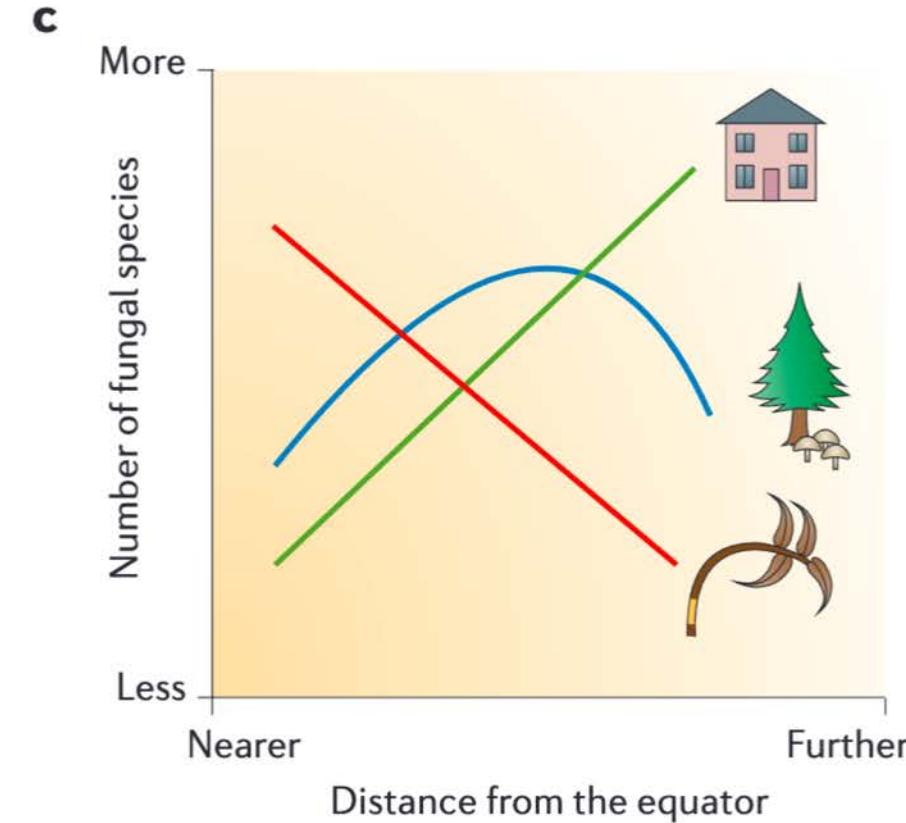
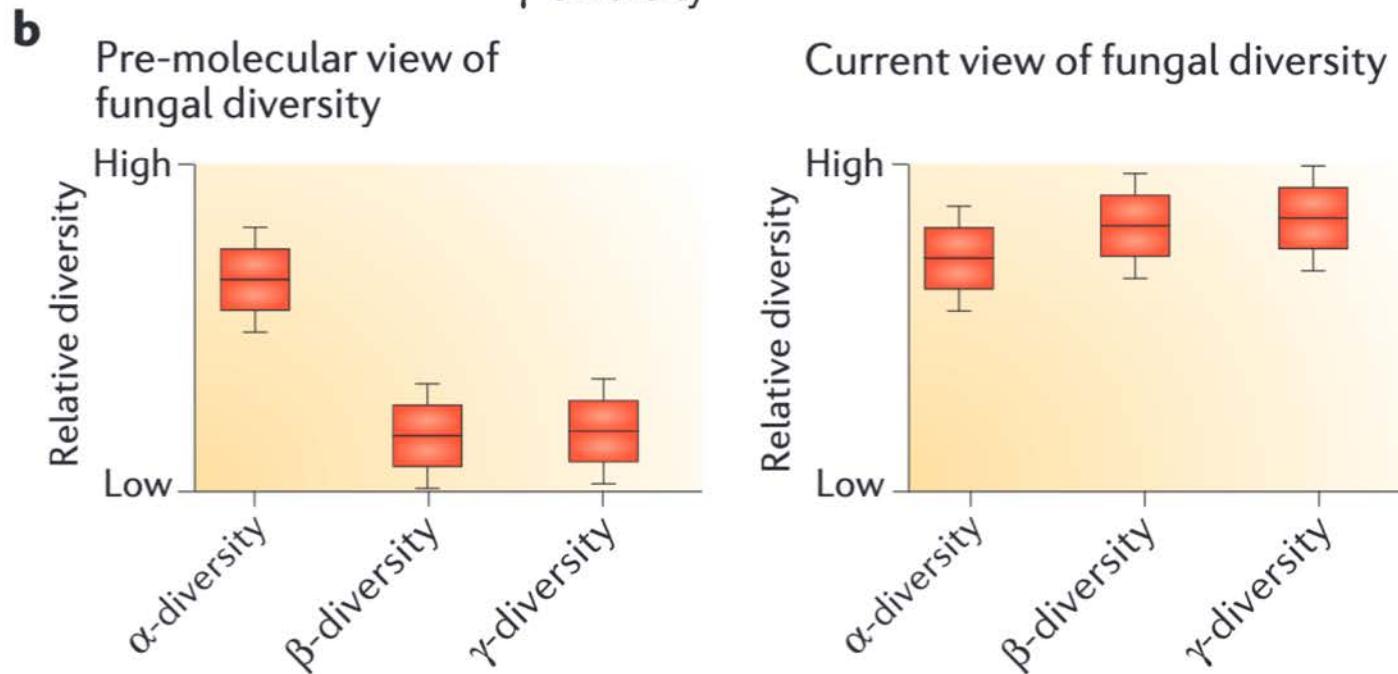
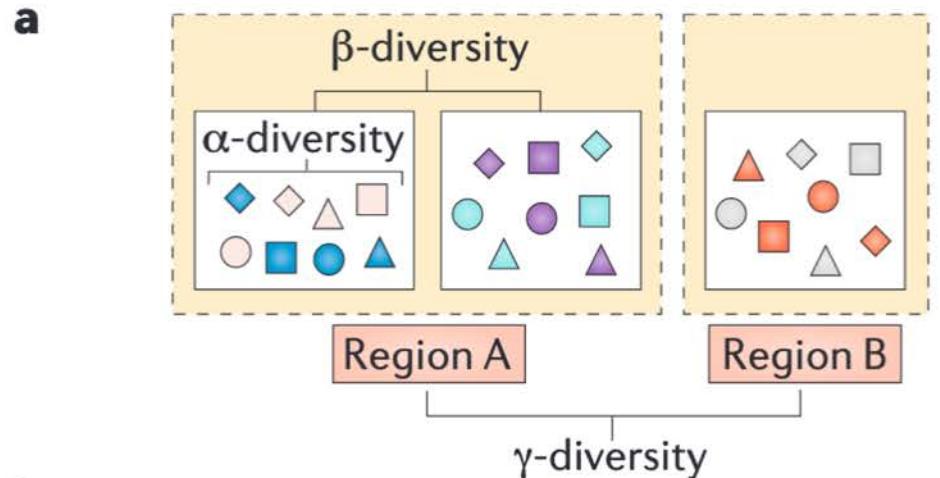
Cattle lungworm *Dictyocaulus viviparus*

#Pilobolus and Lungworm Larvae
<https://www.youtube.com/watch?v=4LrWjnYyc28>

Actively utilize *Pilobolus* to disperse



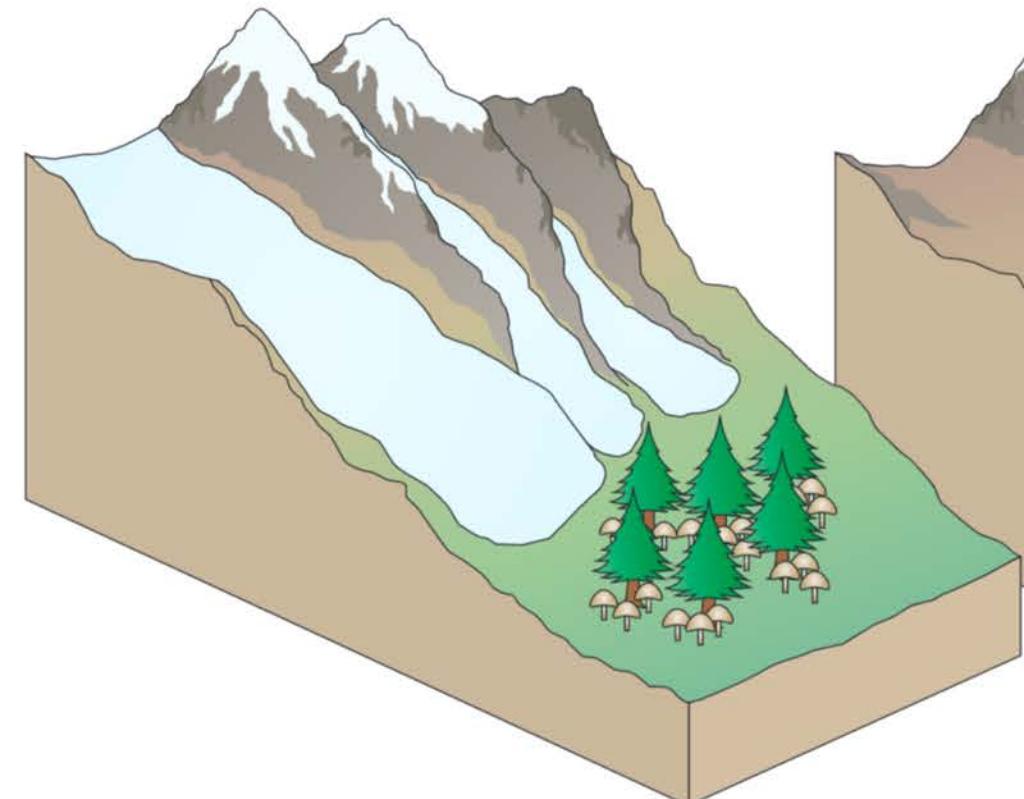
Biogeography and emerging views of fungal diversity



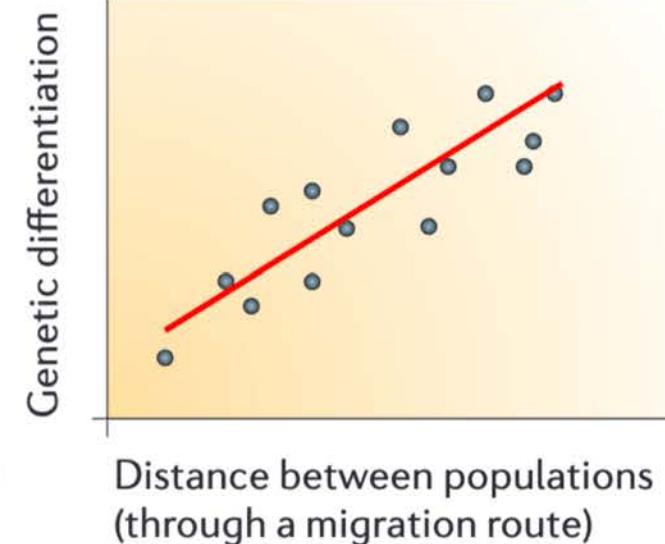
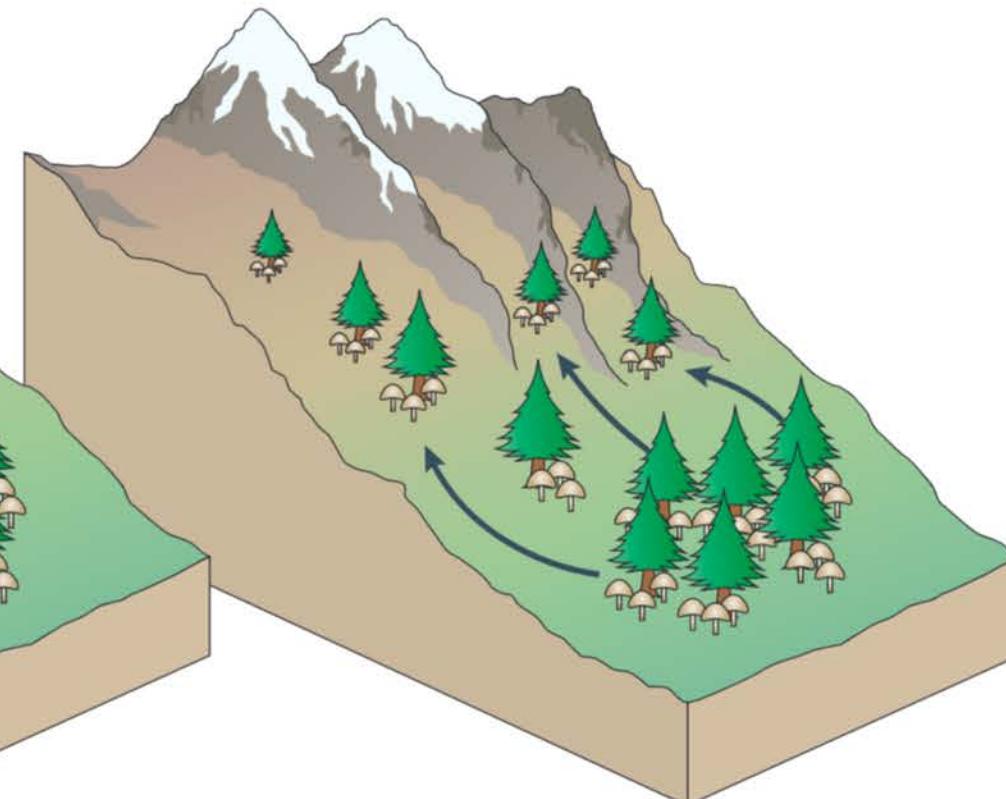
The evolution of new species or genetic diversity in fungi is often associated with dispersal or migration into new habitats

d

Glacial refugium



Post-glacial co-migration



How fungi are engaged in ecosystem processes

1. Primary production
 - a. Making nutrients available for plant growth
 - b. Enhancing nutrient uptake in the rhizosphere
2. Secondary production
 - a. Providing food for both vertebrate and invertebrate animals
 - b. Other fungal/faunal interactions
3. Population and community regulation by plant and animal pathogens
4. Interactions between fungi and human activities
 - a. Pollution
 - b. The built environment

Ecosystem Service	Fungal Functional Group
Soil formation	Lichens Saprotophys Mycorrhizae
Rock dissolution	Saprotophys Mycorrhizae
Particle binding	Saprotophys Mycorrhizae
Providing fertility for primary production	Decomposition or organic residues and nutrient mineralization Soil stability (aggregates)
Primary production	(Ericoid and ectomycorrhizae) Saprotophys Arbuscular mycorrhizae
Direct production	Lichens
Nutrient accessibility	Mycorrhizae Endophytes
Plant yield	Mycorrhizae
Defense against pathogens	Pathogens
Defense against herbivory	Mycorrhizae Pathogens
Plant–plant interactions	Endophytes
As a food source	Saprotophys Mycorrhizae
Population/biomass regulation	Pathogens
Modification of pollutants	Saprotophys Mycorrhizae
Carbon sequestration and storage	Mycorrhizae (Saprotophys)
Decay of human structures and artifacts	Saprotophys

Note: Fungal groups in parentheses are regarded as being of lesser importance in that function.

The good



At least 350 species
are consumed as foods



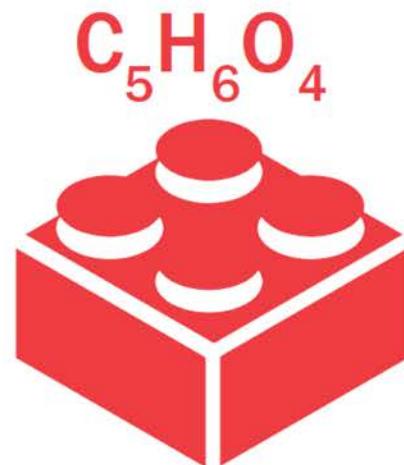
15% of all vaccines
and therapeutic proteins
are made in yeast



Fungi are being used
to turn crop waste
into bioethanol



216 species of fungi
are thought to
be hallucinogenic



Itaconic acid from
fungi is used to
make Lego®

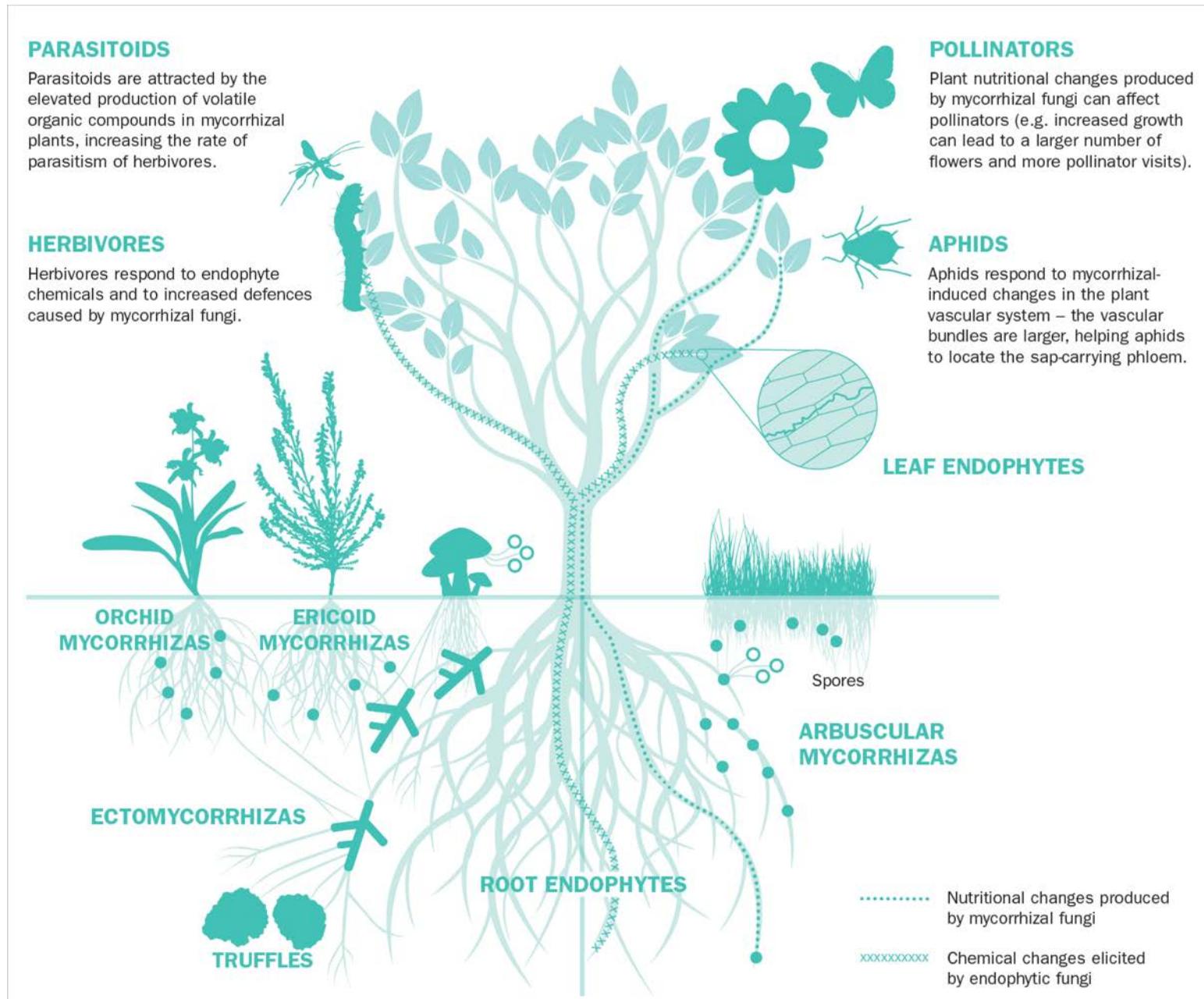
AGRICULTURE	Species of <i>Trichoderma</i> are used to enhance the growth of crops and as a source of enzymes added to improve animal feeds ^[49,50] . Fungi are also the source of an important class of agricultural fungicides called strobilurins ^[51] . <i>Aspergillus flavus</i> is used as a biocontrol agent on peanut crops to out-compete aflatoxin-producing fungi ^[52] .
BEVERAGES	Yeasts underpin alcoholic drink production from beer to wine to spirits. Soft drinks contain citric acid that is produced from the fermentation of <i>Aspergillus niger</i> ^[53] . Glucoamylase from species of <i>Aspergillus</i> is used to convert starch to high-fructose corn syrup, which is used as a sweetener in soft drinks ^[54] .
BIOFUELS	Second-generation bioethanol makes use of species of <i>Trichoderma</i> to break down agricultural waste such as maize straw into sugars that can be fermented using yeast to produce ethanol ^[42] .
BIOREMEDIATION	White rot fungi, including <i>Pleurotus ostreatus</i> and <i>Trametes versicolor</i> , can degrade toxic polychlorinated biphenyl (PCB) chemicals in soil and polluted wastewaters ^[55,56] .
COTTON PROCESSING	Catalase enzymes from species of <i>Aspergillus</i> are used to break down excess bleach in the wastewater from cotton processing ^[57] . <i>Trichoderma</i> cellulases are used to remove fine cotton threads, which prevents the fibre aggregating into pills ^[57] .
FOOD	At least 350 edible mushroom species are known to be collected for food ^[2] . The meat substitute Quorn™ is manufactured using a fungus (<i>Fusarium venenatum</i>) ^[5] . Moulds such as <i>Penicillium camemberti</i> and <i>P. roqueforti</i> are integral to the ripening process in many types of cheese ^[6] . Live yeast and fungal enzymes are used in breadmaking ^[58] . The food colourings lycopene and beta-carotene are now produced from the fungus <i>Blakeslea trispora</i> ^[59] . Soy sauce is produced using koji (<i>Aspergillus oryzae</i>) and the Asian snack tempeh makes use of <i>Rhizopus microsporus</i> ^[60,61] .
HALLUCINOGENS	Worldwide, 216 species of fungi are believed to be hallucinogenic – of these, 116 species belong to the genus <i>Psilocybe</i> ^[62] .
LEATHER PROCESSING	Leather hides are degreased with lipase enzymes from <i>Aspergillus oryzae</i> ^[63,64] .

MEDICINES	Many drugs come from fungi. Penicillin from <i>Penicillium rubens</i> revolutionised the treatment of bacterial infections and cyclosporine from <i>Tolypocladium inflatum</i> made organ transplantation possible ^[11–13] . Gestodene is an active ingredient in third-generation contraceptive pills; a key step in its synthesis is achieved using fungal fermentation with <i>Penicillium raistrickii</i> ^[65] .
PAPER MANUFACTURING	Cellulase enzymes produced by species of <i>Trichoderma</i> and <i>Humicola</i> are used to speed up the pulping process thereby reducing water usage ^[37,38] .
PLASTICS AND BIOMATERIALS	Plastic car parts, synthetic rubber and Lego™ are made using itaconic acid derived from species of <i>Aspergillus</i> ^[66,67] . Additionally, fungal mycelium-based products are now being used as replacements for polystyrene foam, leather and building materials ^[68–70] .
RESEARCH	Since 2010, more than a quarter of Nobel prizes for physiology or medicine were awarded for work based on yeast ^[71] .
VITAMINS	The vitamin B2 used for vitamin supplements is produced by fermentation of the fungus <i>Eremothecium gossypii</i> ^[72] .
WASHING DETERGENTS	Cellulase enzymes produced by the thermophilic fungus <i>Humicola insolens</i> are added to washing powders and liquids. They trim the fine cotton threads on the surface of cotton fabric to produce a smoother, newer feel ^[41,73] . Lipase enzymes from the same species are also added to break down fat stains ^[40,41] .

PLANT–FUNGAL MUTUALISMS

1. Endophytes
can be beneficial to plant
growth, especially in harsh
environments

2. Mycorrhizas.
key benefits to terrestrial
ecosystems, including: (i)
enhanced nutrient uptake,
(ii) soil structure; and (iii)
carbon sequestration,



The bad

Ophiocordyceps unilateralis



Andersen *et al.*, Am Nat (2009)

BOX 1: FROM FUNGAL IMMUNOSUPPRESSANT TO BILLION-DOLLAR DRUG

The entomopathogenic fungus *Isaria sinclairii* infects cicada larvae; it grows inside its host, initially without killing it but instead replacing the host tissue with fungal mycelium.

Eventually its spore-bearing structures emerge from the dead larvae. *Isaria sinclairii* produces an immunosuppressant chemical compound called myriocin. Extensive chemical redesign of myriocin resulted in the immunosuppressive multiple sclerosis treatment fingolimod. Fingolimod is a blockbuster drug with sales of US\$2.48 billion in 2018^[83].



Fungi can even consume nematodes (線蟲)

<https://vimeo.com/125211921>

REVIEW

doi:10.1038/nature10947

Emerging fungal threats to animal, plant and ecosystem health

Matthew C. Fisher¹, Daniel. A. Henk¹, Cheryl J. Briggs², John S. Brownstein³, Lawrence C. Madoff⁴, Sarah L. McCraw⁵
& Sarah J. Gurr⁵

Plant pathogens

<i>Sporisorium scitamineum</i> (Sscl8)	Sugar cane	Sugar cane	Biotroph	Sexual	20	6.7	Repeat-rich gene clusters that encode effector candidates	48
<i>Ustilago maydis</i> (521)	Maize	Maize	Biotroph	Sexual	20	6.7	Repeat-rich gene clusters that encode effector candidates	48, 66
<i>Microbotryum lychnidis-dioicae</i> (p1A1 Lamole)	Red campion	Red campion	Biotroph	Sexual	33	14	Repeat-rich gene clusters that encode effector candidates	103, 104
<i>Melampsora larici-populina</i> (98AG31)	Poplar and larch	Poplar and larch	Biotroph	Sexual and asexual	101	45	ND [#]	73
<i>Puccinia graminis</i> f.sp. <i>tritici</i> (CDL75-36-700-3, race SCCL)	Wheat	Wheat and barley	Biotroph	Sexual and asexual	89	45	Highly polymorphic effector candidates	73
<i>Zymoseptoria tritici</i> (IPO323)	Wheat	Wheat	Hemi-biotroph	Sexual and asexual	40	<ul style="list-style-type: none"> • 18.6 (genome mean) • 16.6 (core) • 33.6 (accessory) 	<ul style="list-style-type: none"> • Orphan regions are enriched in <i>in planta</i>-expressed genes • Possible function of accessory chromosomes in virulence 	45, 57, 58
<i>Leptosphaeria biglobosa</i> 'canadensis' (J154)	Mustard	Crucifers	Necrotroph	Sexual and asexual	32	3.9	ND [#]	71
<i>Leptosphaeria maculans</i> 'brassicae' (v23.1.3)	Oilseed rape	Crucifers	Hemi-biotroph	Sexual and asexual	45	35.5 (99.8% of all repeats located in AT-isochores)	<ul style="list-style-type: none"> • Enrichment of effector candidates and chromatin-mediated effector candidate regulation in AT isochores • Conditionally dispensable chromosome contains avirulence-encoding gene 	29, 60

Plant pathogens

effectors							
<i>Blumeria graminis f. sp. hordei</i> (DH14)	Barley	Various	Biotroph	Sexual and asexual	120	64	Repeat-rich accessory regions that encode infection-specific transcribed genes 142
<i>Magnaporthe oryzae</i> (70–15)	Rice	Various crops and wild grasses	Hemi-biotroph	Sexual and asexual	41	10	Highly polymorphic effector candidates and translocations of effector genes 22, 143
<i>Ophiostoma novo-ulmi</i> (H327)	Elm	Elm	Necrotroph	Sexual and asexual	32	3.4	ND [#] 144
<i>Verticillium dahliae</i> (VdLs17)	Lettuce	Various	Necrotroph	Asexual	37	12	Enrichment of <i>in planta</i> -expressed effector candidates in LS [#] regions 16, 44
<i>Fusarium solani</i> /Nectria haematococca MPVI (77-13-4)	Pea	Various	Hemi-biotroph	Sexual and asexual	54	• <5 (core) • >10–25 (supernumerary)	LS chromosomes confer host specificity and virulence 46
<i>Fusarium graminearum</i> (PH-1)	Wheat	Wheat and barley	Hemi-biotroph	Sexual and asexual	36	<3	Enrichment of <i>in planta</i> -expressed and species-specific genes in regions of high SNP [#] density 145
<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> (4287)	Tomato	Various	Hemi-biotroph	Asexual	60	28 (~74% of TEs [#] located on LS [#] chromosomes)	LS chromosomes confer host specificity and virulence 43

LS, lineage-specific; ND, no data; TEs, transposable elements. *Genome size and repeat content refer to the respective reference isolate. Isolate-specific hosts refer to the host plant from which the reference isolate was collected. In some cases, other isolates of the same species infect other hosts. [#]Genome characteristics have been inferred from comparative genomics analyses.

Corn smut *Ustilago*



Photo by David Cohen/flickr/CC BY 2.0

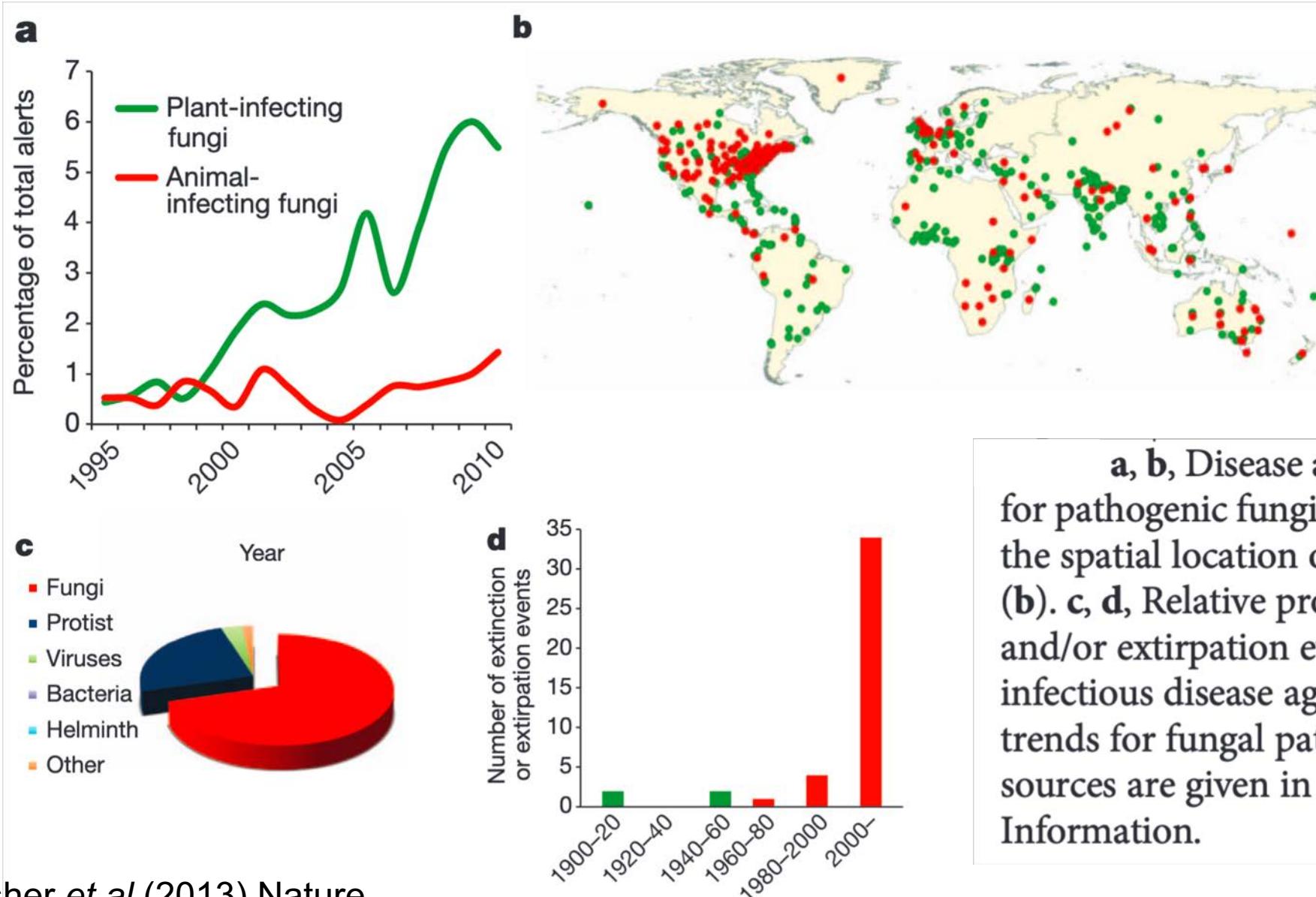


Zizania latifolia infected by
Ustilago esculenta

Animal pathogens

	Host	Pathogen (Phylum)	Disease dynamics leading to mass mortality in animal and plant hosts
	Amphibian species (for example, the common midwife toad, <i>Alytes obstetricans</i>)	<i>Batrachochytrium dendrobatidis</i> (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 ^{15,82} .
	Coral species (for example, the sea fan, <i>Gorgonia ventalina</i>)	<i>Aspergillus sydowii</i> (Ascomycota)	Sea-fan aspergillosis caused by a common terrestrial soil fungus ^{21,86} . 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 (<i>Apis mellifera</i>) suffering colony collapse disorder)	<i>Nosema</i> 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 ^{87,88} .

Worldwide reporting trends in fungal Emerging Infectious Diseases (EIDs)



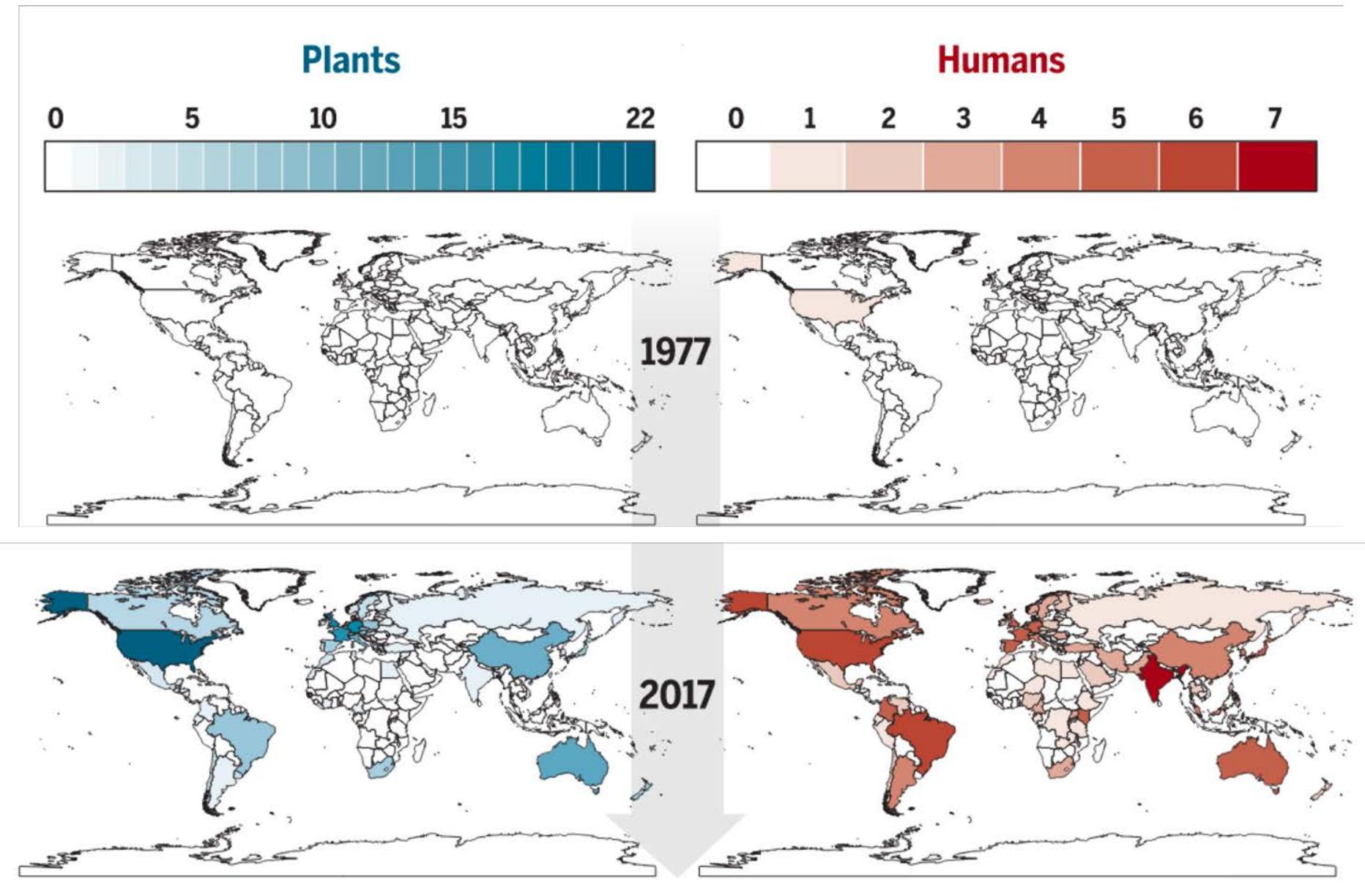
a, b, Disease alerts in the ProMED database for pathogenic fungi of animals and plants (**a**), and the spatial location of the associated reports (**b**). **c, d**, Relative proportions of species extinction and/or extirpation events for major classes of infectious disease agents (**c**) and their temporal trends for fungal pathogens (**d**). Primary data sources are given in the Supplementary Information.

Worldwide emergence of resistance to antifungal drugs challenges human health and food security

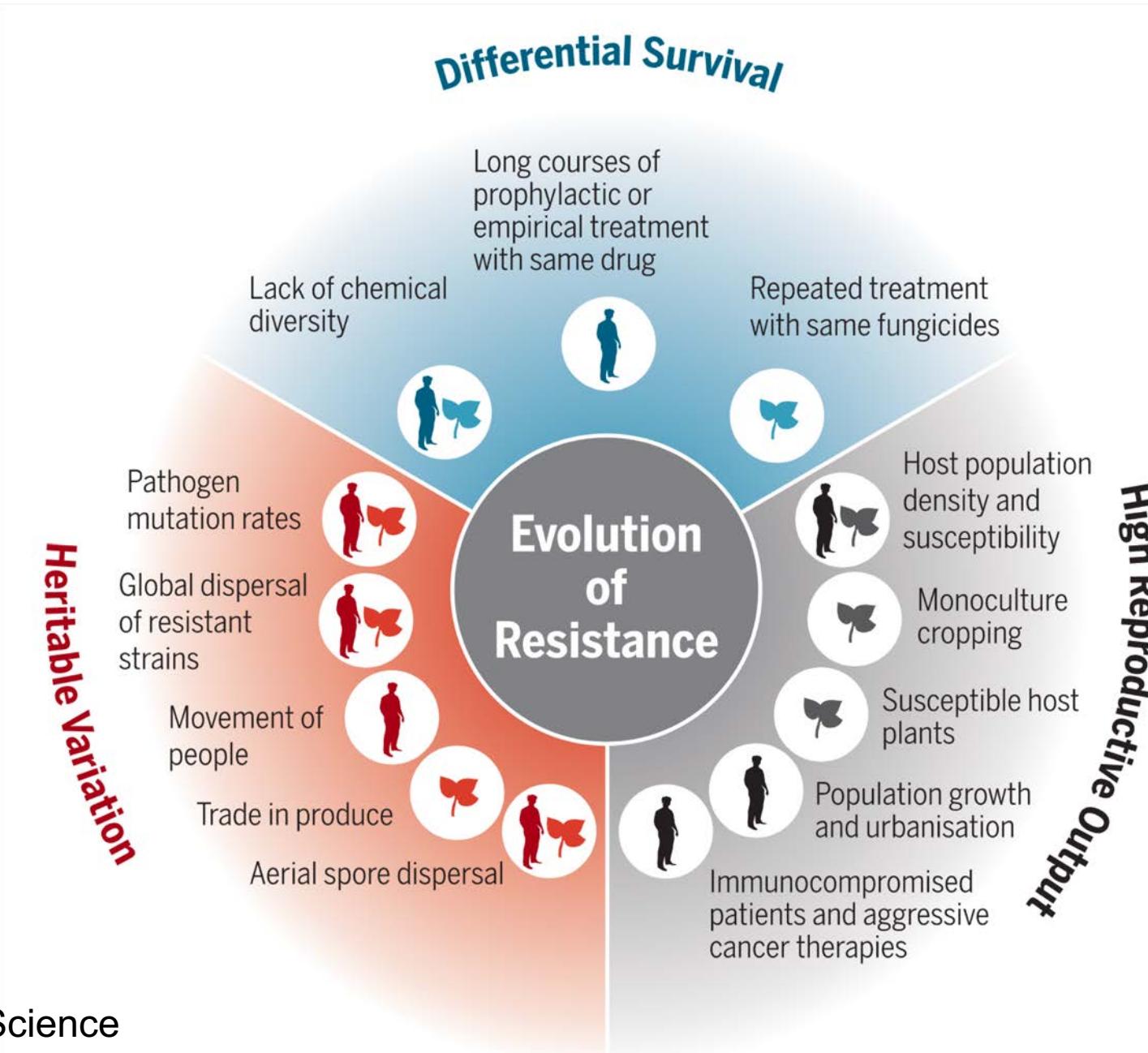
Matthew C. Fisher,^{1,*} Nichola J. Hawkins,² Dominique Sanglard,³ Sarah J. Gurr^{4,5,*}

The recent rate of emergence of pathogenic fungi that are resistant to the limited number of commonly used antifungal agents is unprecedented. The azoles, for example, are used not only for human and animal health care and crop protection but also in antifouling coatings and timber preservation. The ubiquity and multiple uses of azoles have hastened the independent evolution of resistance in many environments. One consequence is an increasing risk in human health care from naturally occurring opportunistic fungal pathogens that have acquired resistance to this broad class of chemicals. To avoid a global collapse in our ability to control fungal infections and to avoid critical failures in medicine and food security, we must improve our stewardship of extant chemicals, promote new antifungal discovery, and leverage emerging technologies for alternative solutions.

Fungal species with reported antifungal resistance, by country



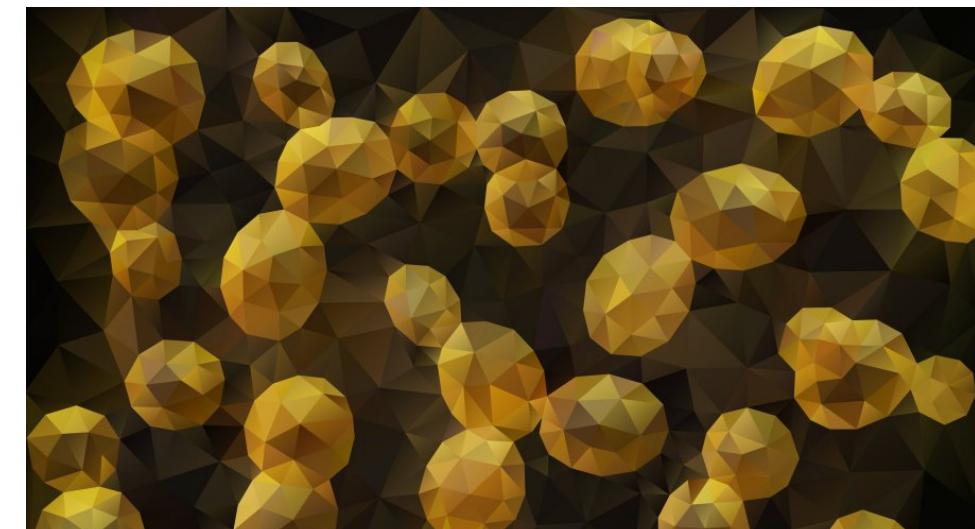
Evolutionary drivers of antifungal resistance



How do we study all these?

Model organisms

- Easy to maintain and breed in a laboratory setting.
- Many model organisms can breed in large numbers.
- Some have a very short generation time, which is the time between being born and being able to reproduce, so several generations can be followed at once
- Mutants allow scientists to study certain characteristics or diseases.
- Easy and cheap genetic manipulation
- Some model organisms have orthologs to humans.
- Model organisms can be used to create highly detailed genetic maps.
- Or they may occupy a pivotal position in the evolutionary tree



Research in model yeast *Saccharomyces cerevisiae*

Yeast: An Experimental Organism for 21st Century Biology

David Botstein^{*,1} and Gerald R. Fink[†]

^{*}Lewis-Sigler Institute for Integrative Genomics, Princeton University, Princeton, New Jersey 08544, and [†]Whitehead Institute for Biomedical Research and Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

Functional Genomics: Gene–Protein–Function Association via Mutants

Databases and Gene Ontology

Gene Expression and Regulatory Networks

Protein Interaction Networks

Gene Interaction Networks

Integrating Co-expression and Protein and Gene Interaction Networks

Leveraging Diversity to Understand Complex Inheritance

Strengths and Weaknesses of Genome-Scale Experimentation and Inference: Experimental Validation Is Essential

Evolution

Evidence for the theory of duplication and divergence

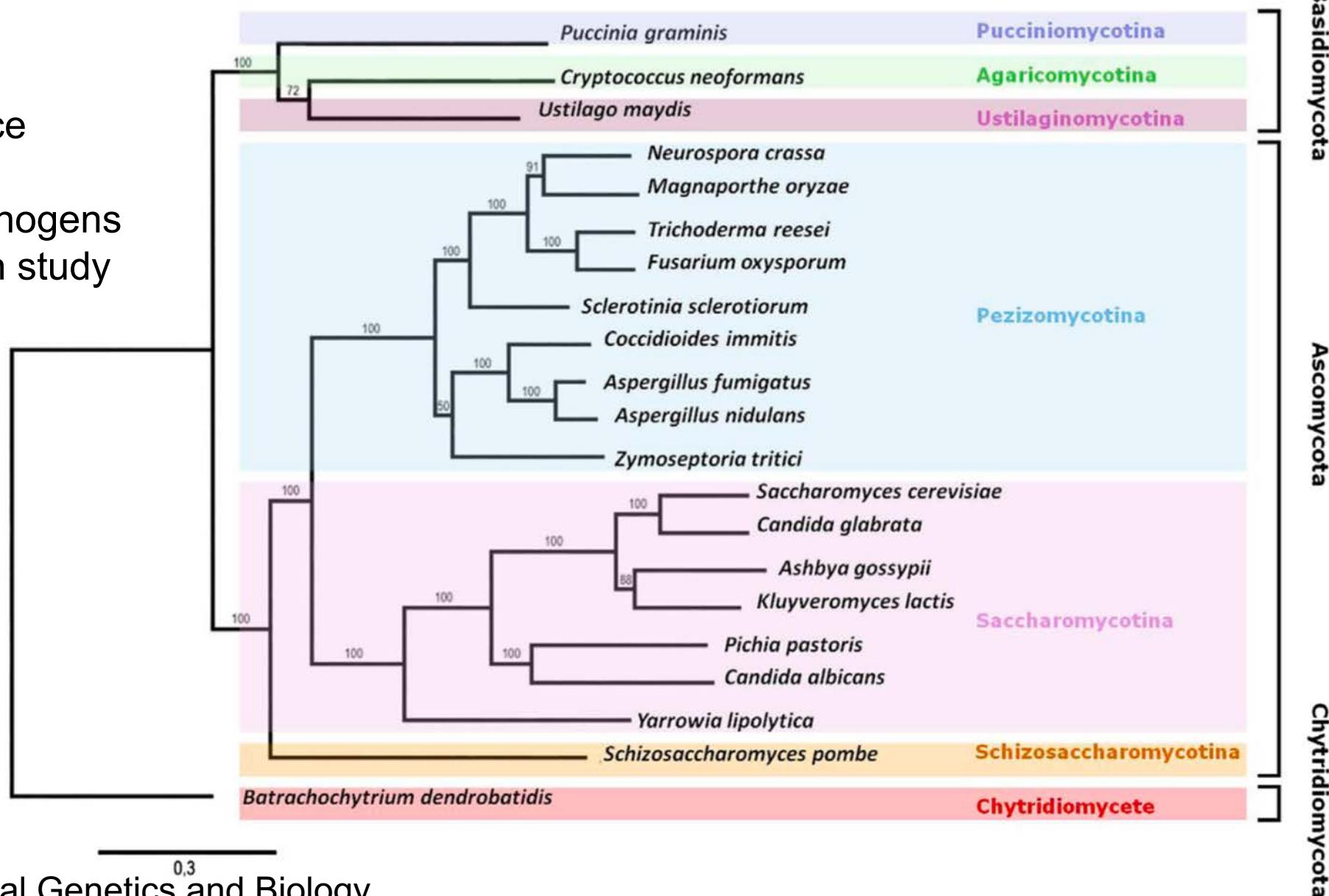
Experimental evolution studies with yeast

Human Disease

- Biotechnology
- Fermentation
- Synthetic biology
- High-throughput / Systematic
- Light sensing

Research in other model fungi

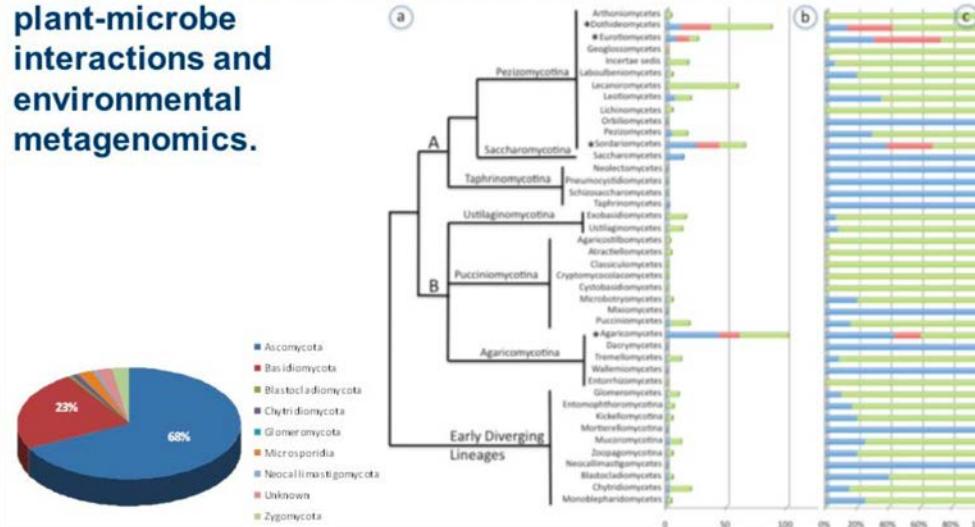
- All have genome sequence available
- Most are animal/plant pathogens
- So much emphasis put on study of virulence



Fungal genomes



Goal: Sequencing 1000 fungal genomes from across the Fungal Tree of Life will provide references for research on plant-microbe interactions and environmental metagenomics.



SCIENTIFIC REPORTS

OPEN

The Genome Sequences of 90 Mushrooms

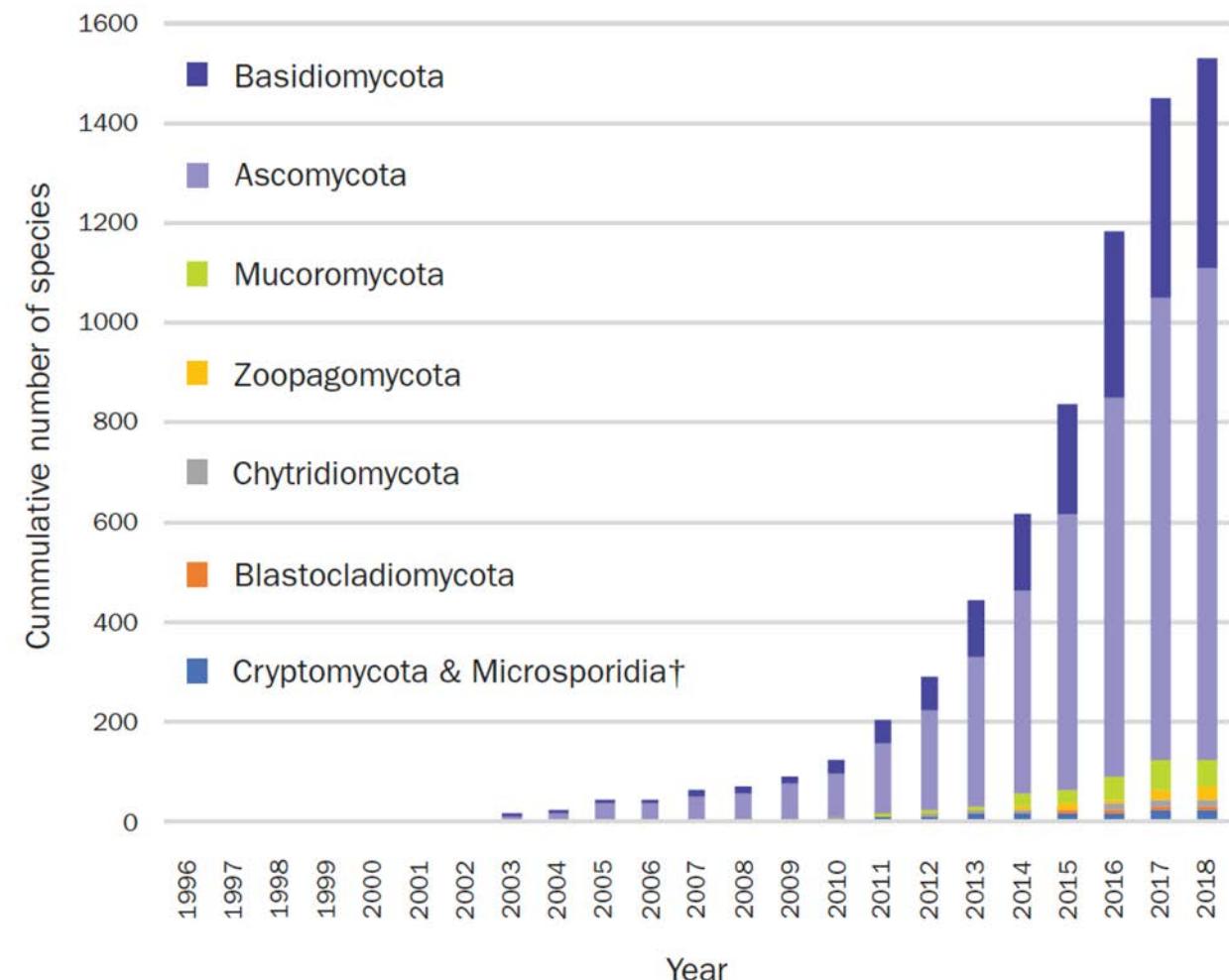
Huiying Li¹, Surui Wu³, Xiao Ma^{4,5}, Wei Chen^{2,4}, Jing Zhang⁶, Shengchang Duan⁶, Yun Gao⁶, Ling Kui^{7,8}, Wenli Huang¹², Peng Wu⁴, Ruoyu Shi^{4,5}, Yifan Li⁵, Yuanzhong Wang⁹, Jieqing Li⁹, Xiang Guo³, Xiaoli Luo³, Qiang Li¹², Chuan Xiong¹², Honggao Liu⁹, Mingying Gui³, Jun Sheng^{4,5} & Yang Dong^{2,10,11}

ed: 4 December 2017

ed: 6 June 2018

FIGURE 1: CUMULATIVE NUMBER OF FUNGAL SPECIES WITH WHOLE-GENOME SEQUENCES

[Data collated from online genome databases including NCBI Genome database (ncbi.nlm.nih.gov/genome), JGI Genome Portal: MycoCosm (genome.jgi.doe.gov/fungi), and EnsembleFungi (fungi.ensembl.org)]

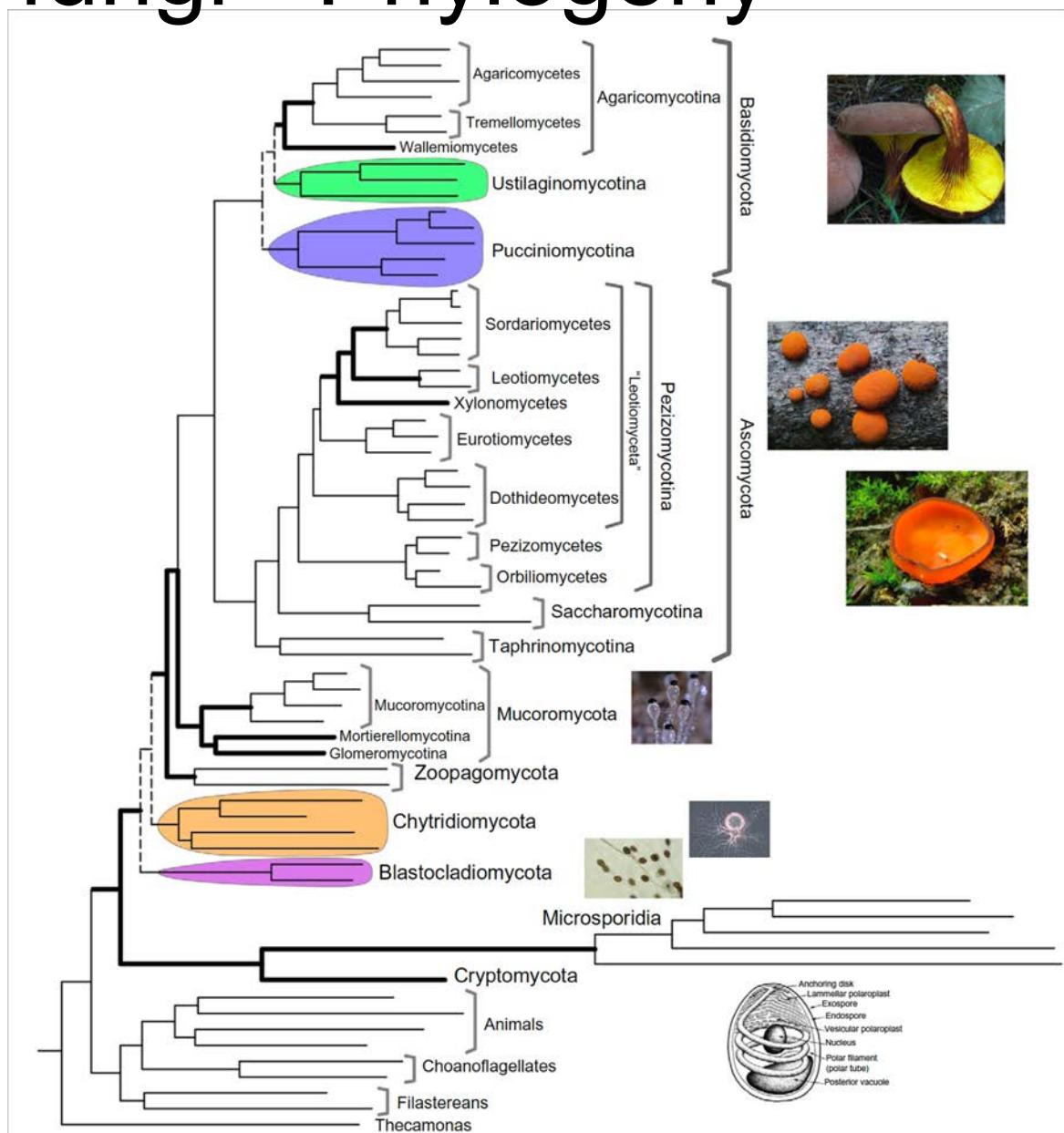


Importance of genomics in fungi - Phylogeny

The accelerating pace of fungal genome sequencing by a number of large-scale sequencing projects paved the way for assembling larger and taxon-specific datasets that clarified some of the puzzling fungal relationships.

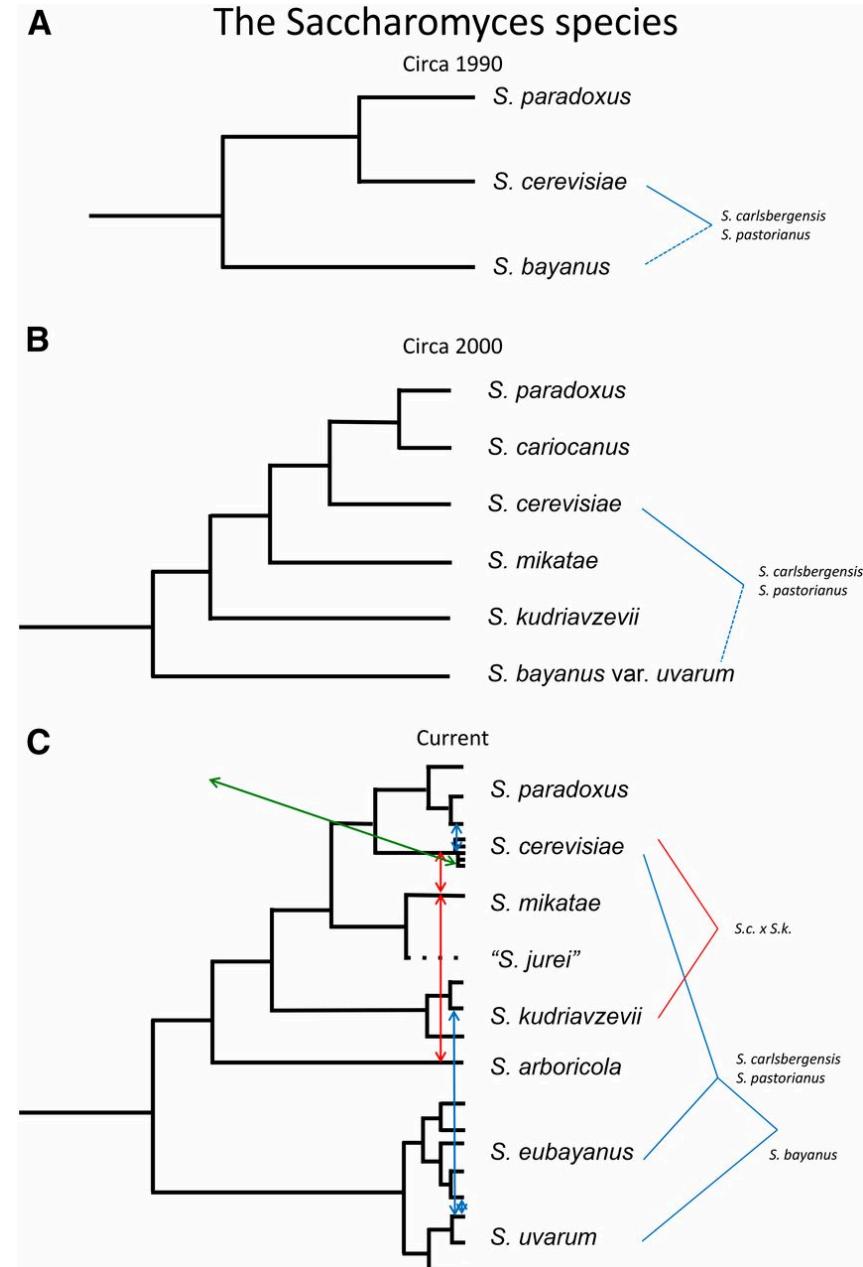
- sister relationship between the Leotiomycetes and Sordariomycetes
- resolved the position of the Xylonomycetes, a small class of leaf endophytes, as a sister group to the Lecanoromycetes and Eurotiomycetes.

Resolving ancient divergences poses significant challenges even for phylogenomic datasets. For example, the definition of the fungal kingdom and the placement of the Microsporidia as fungi or nonfungal eukaryotes have been debated. (to be discussed in the next lecture)



Importance of genomics in fungi - Comparative

- Comparative genomics analysis of *S. cerevisiae* and closely related species has contributed to our understanding of **how new species emerge and has shed light on the various mechanisms that contribute to reproductive isolation.**
- Genomic analysis of *Saccharomyces* yeasts has provided a better understanding of the mechanisms underlying large-scale genomic changes, such as polyploidy, and their consequences for genome evolution and cell physiology.
- Genomic approaches are increasingly contributing to our understanding of how budding yeasts adapt to natural environments by identifying the genes that are involved in adaptation within natural substrates.



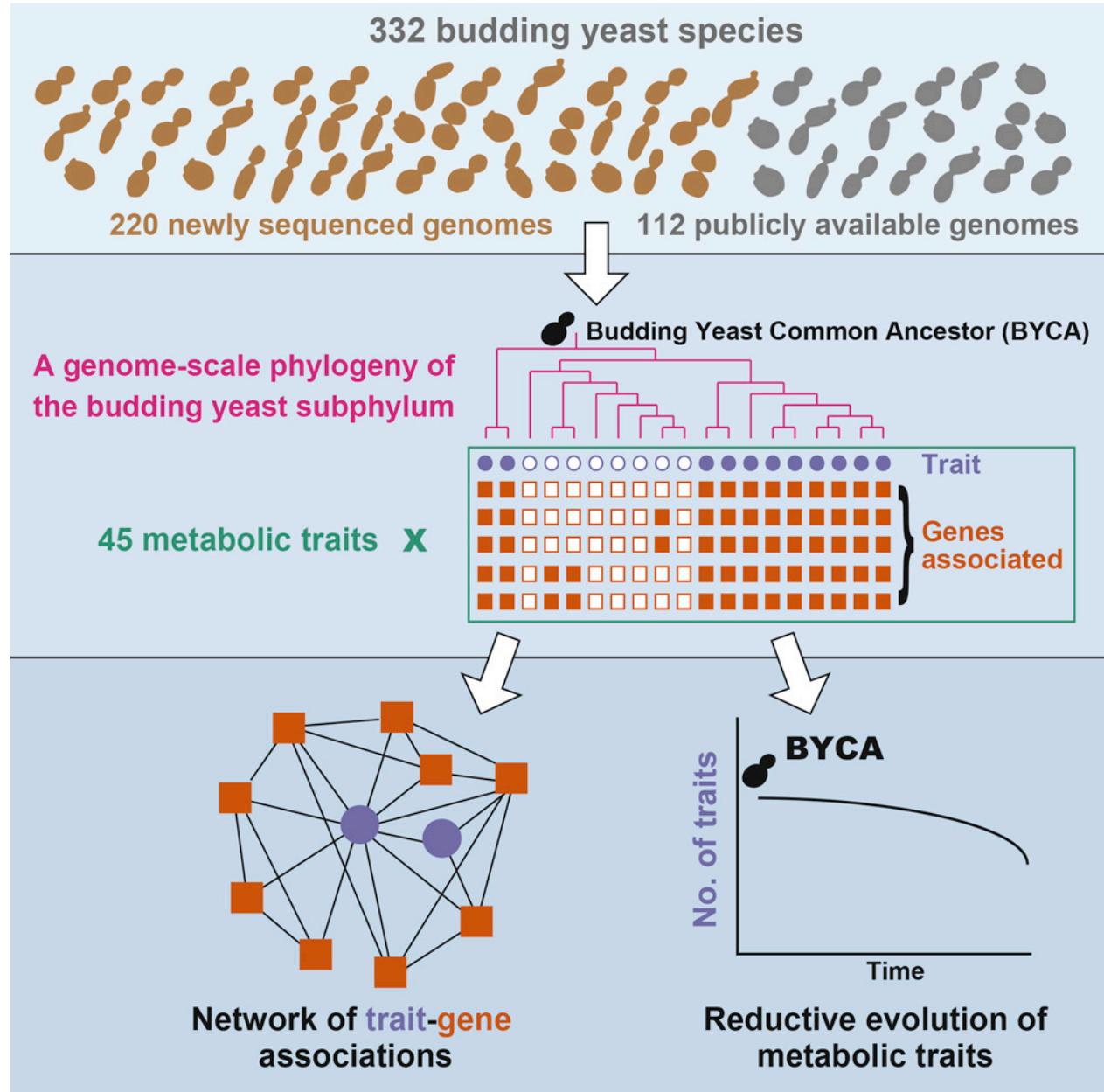
Dujon and Louis (2017) Genetics

Marsit et al (2017) Nature Genetics Review

Importance of genomics in fungi - Comparative (example)

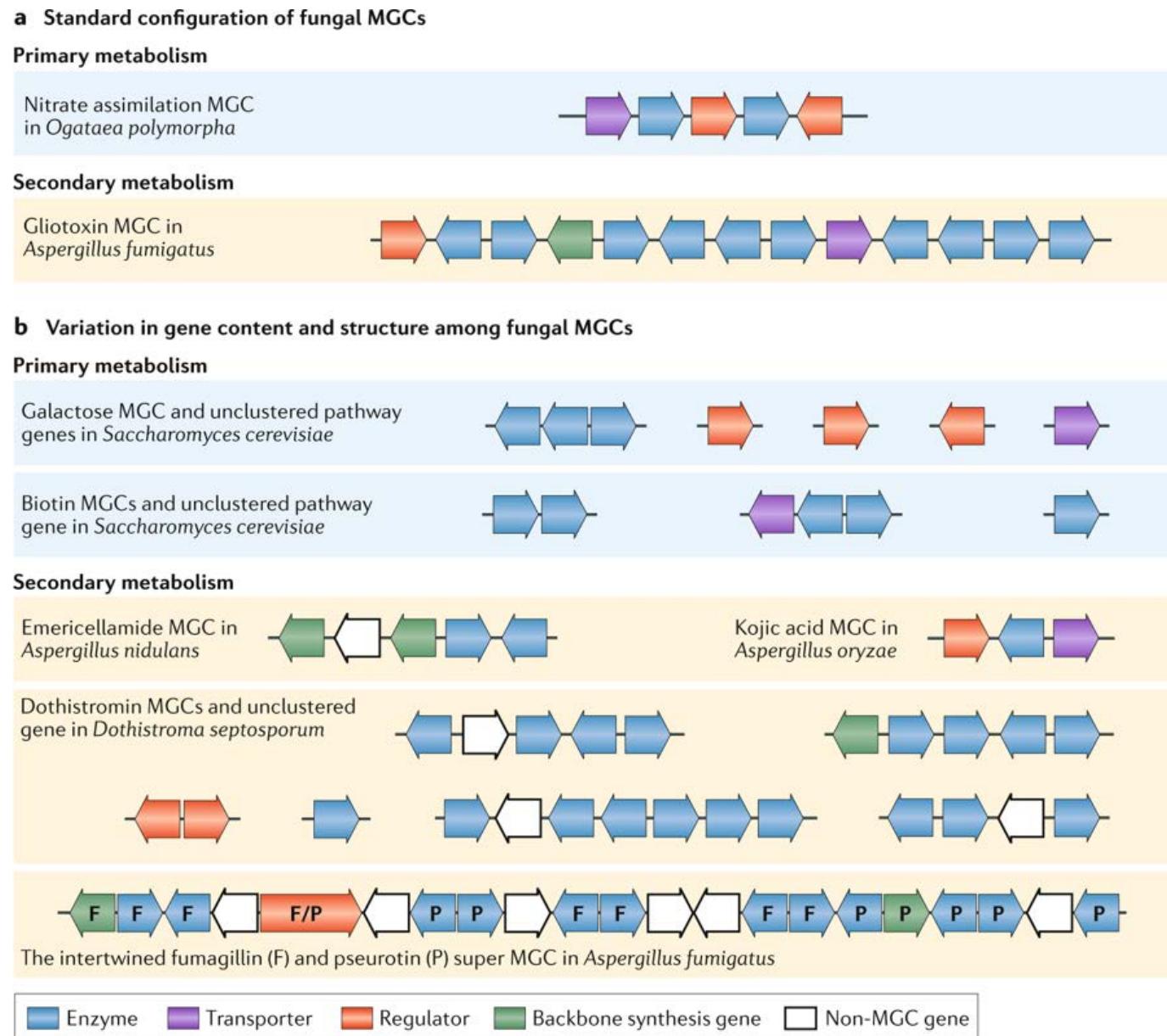
Highlights

- 332 genomes, including 220 newly sequenced, covering ~1/3 of known budding yeasts
- Genome-scale inference of robust phylogeny and time tree of budding yeast subphylum
- Reconstruction of 45 metabolic traits infers complex budding yeast common ancestor
- Reductive evolution of traits and genes is a major mode of evolutionary diversification



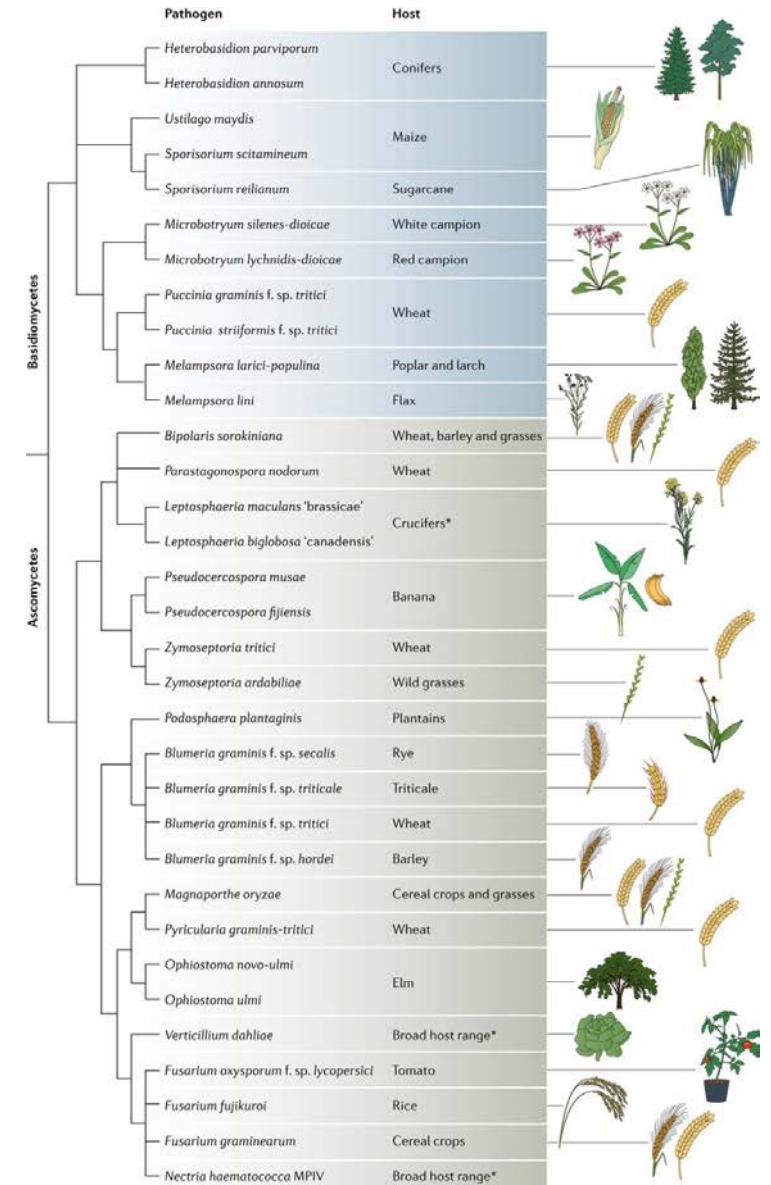
Importance of genomics in fungi - Comparative (example2)

- Fungi contain a remarkable diversity of both primary and secondary metabolic pathways involved in ecologically specialized or accessory functions.
- Genes in these pathways are frequently physically linked on fungal chromosomes, forming metabolic gene clusters (MGCs).
- Improved knowledge of the evolutionary life cycle of MGCs will advance our understanding of the ecology of specialized metabolism and of the interplay between the lifestyle of an organism and genome architecture.



Importance of genomics in fungi – plant pathogens

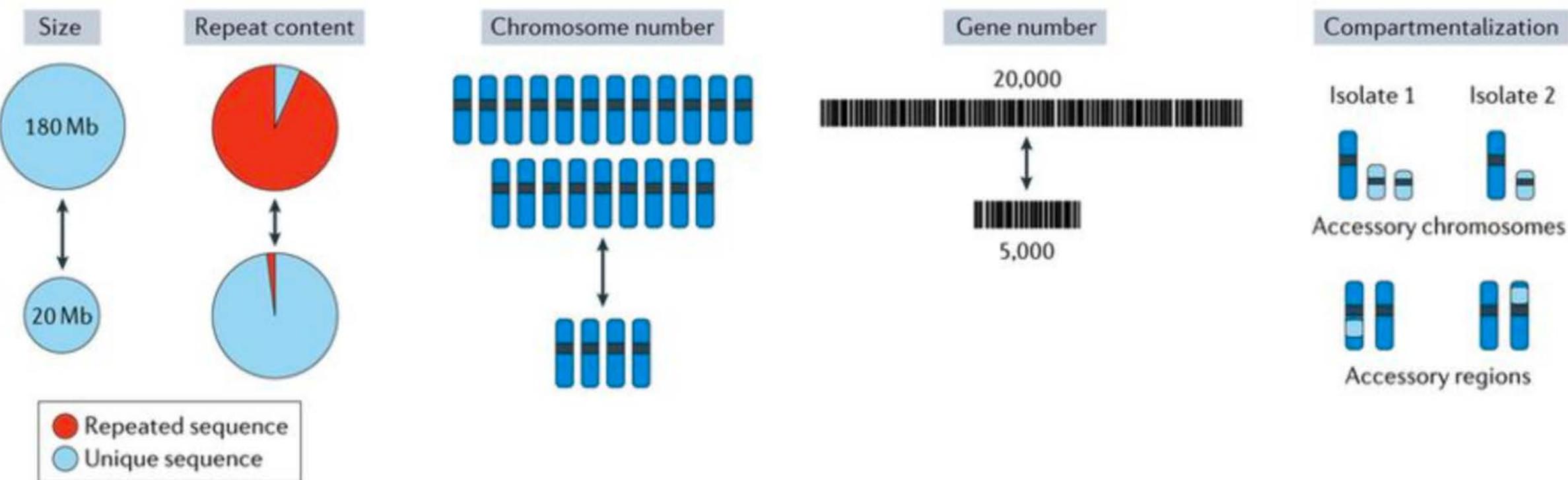
- The genomes of fungal plant pathogens can vary in size and composition, even between closely related species. Differences in the content of transposable elements cause variation in genome architecture.
- Variation in genome architecture results from differences in population genetic factors, including effective population size and the strength of genetic drift.
- During periods of low effective population size, non-adaptive mutations, such as transposable elements, can invade genomes and shape their architecture.
- Transposable elements contribute to the establishment and maintenance of rapidly evolving genome compartments that can comprise virulence genes. High mutation rates in these compartments support the evolution of new virulence phenotypes.



Importance of genomics in fungi – plant pathogens

- The genomes of fungal plant pathogens can vary in size and composition, even between closely related species. Differences in the content of transposable elements cause variation in genome architecture..

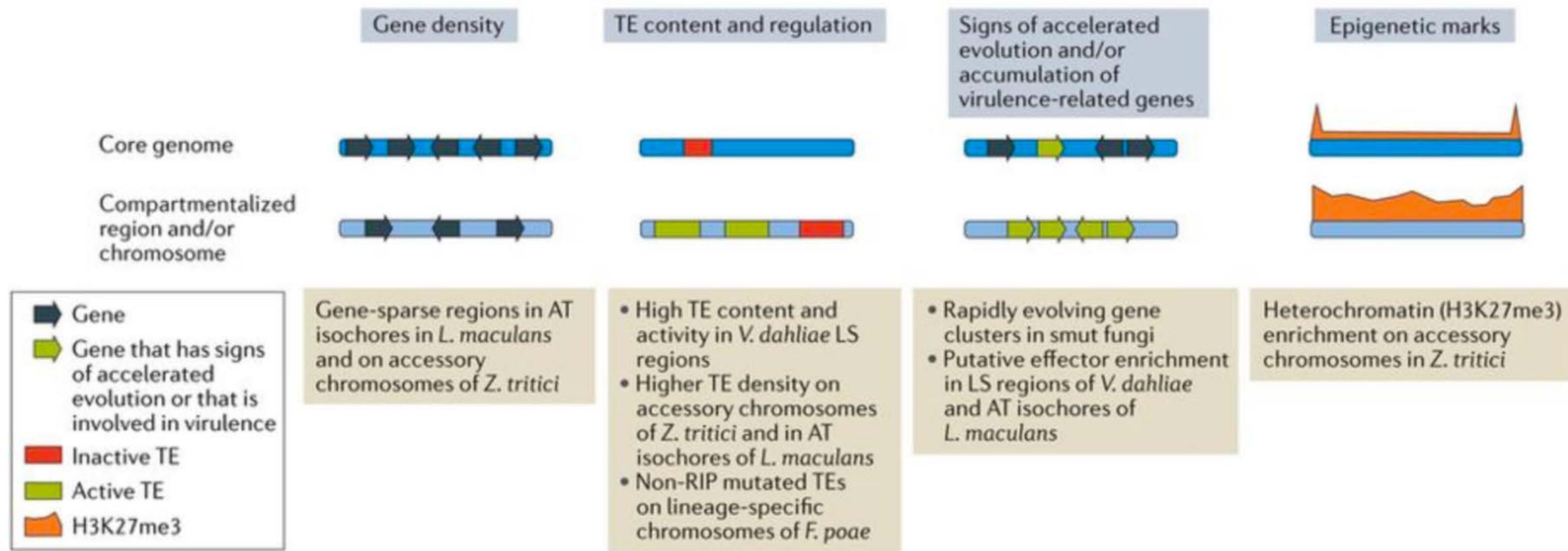
a Fungal plant pathogen genomes are highly diverse



Importance of genomics in fungi – plant pathogens

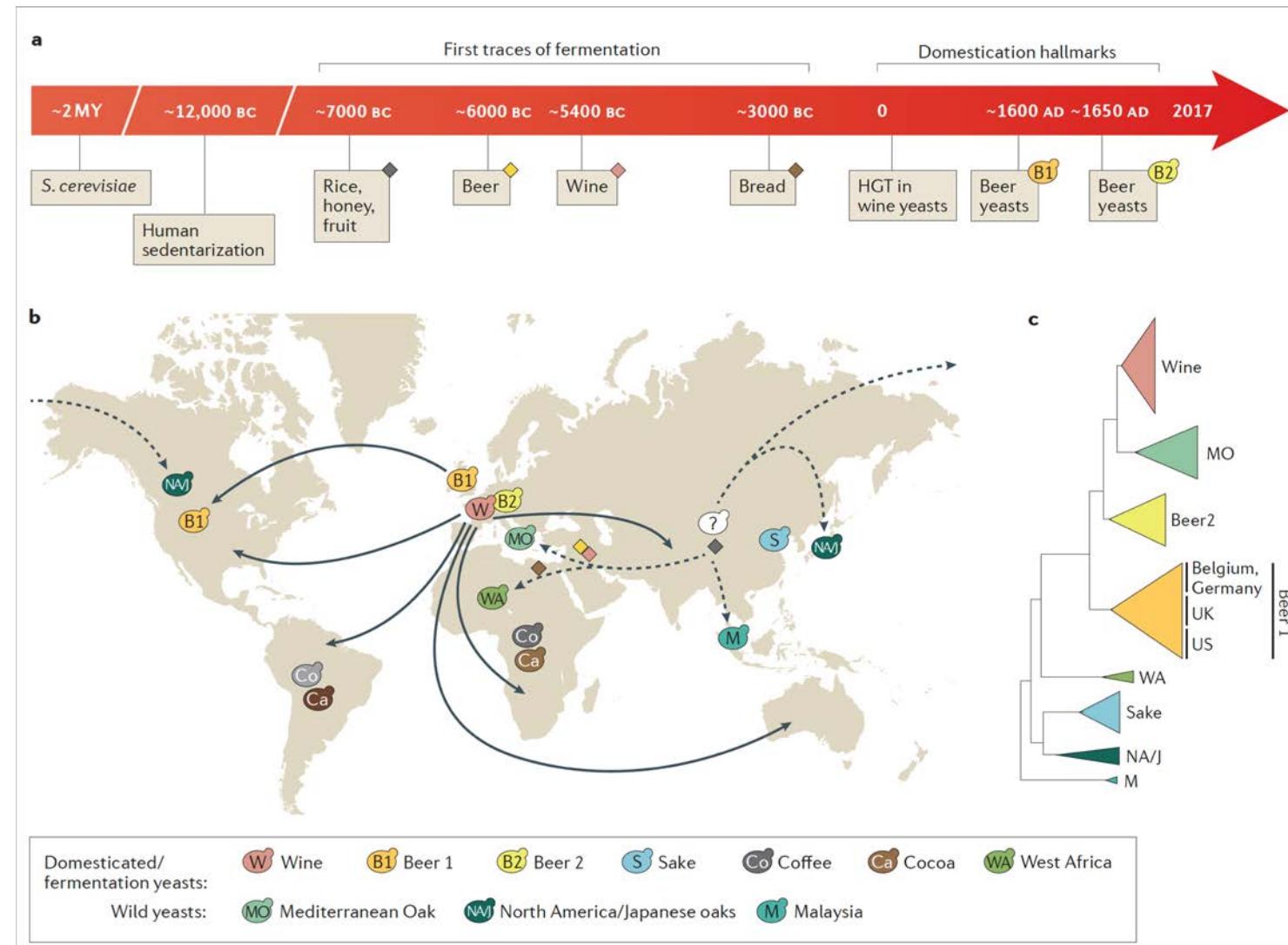
- The genomes of fungal plant pathogens can vary in size and composition, even between closely related species. Differences in the content of transposable elements cause variation in genome architecture..

b Characteristics of genome compartments



Importance of genomics in fungi - Population

- Population genomics and comparative genomics of *Saccharomyces* yeasts have revealed that hybridization occurred frequently throughout, and has had substantial effects on, yeast evolution. Hybridization could itself be a mechanism of adaptation and speciation.
- Genomic analysis of yeast strains associated with humans has revealed the history of yeast domestication and the mechanisms that have contributed to its adaptation to anthropogenic environments.

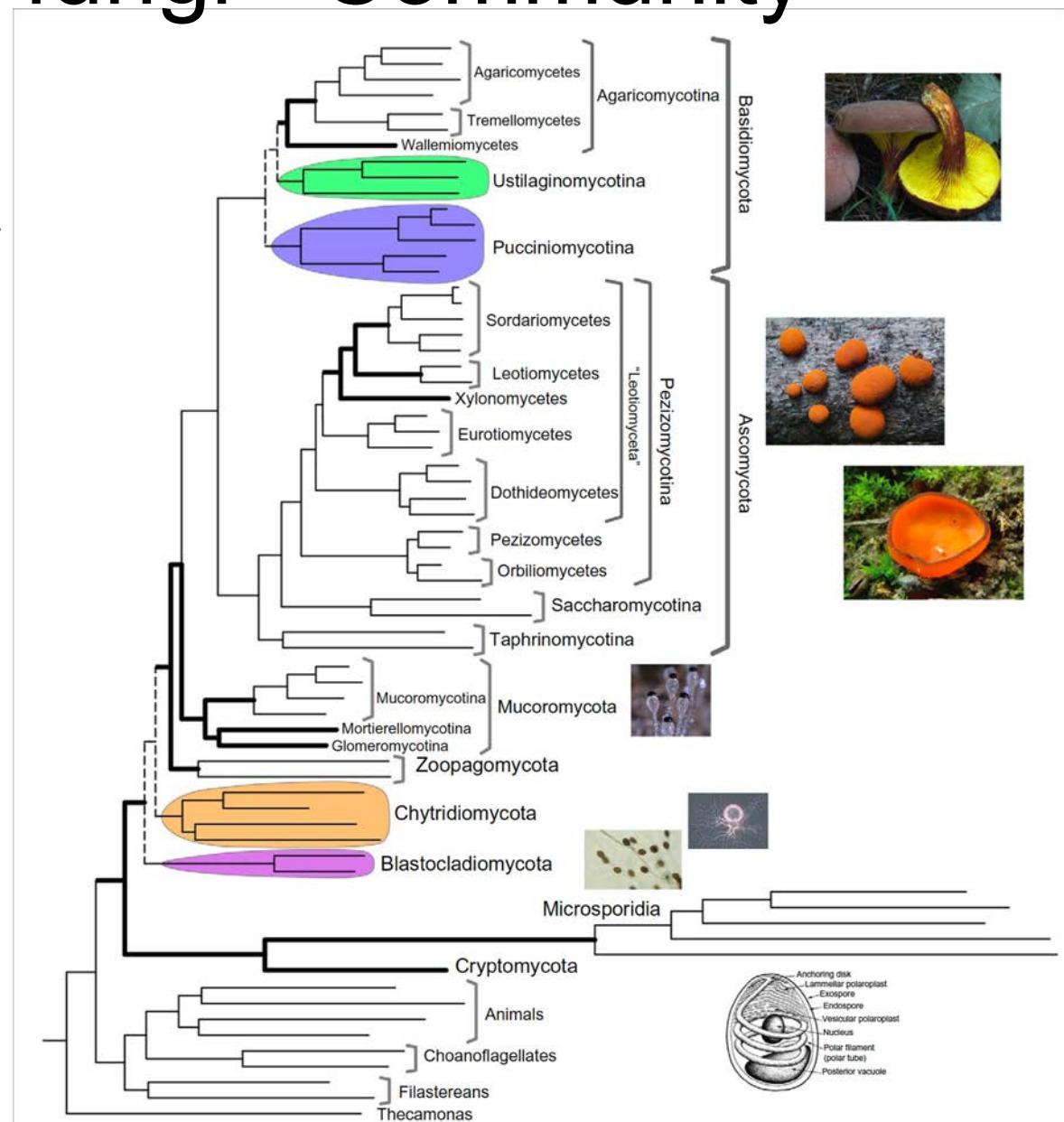


Importance of genomics in fungi - Community

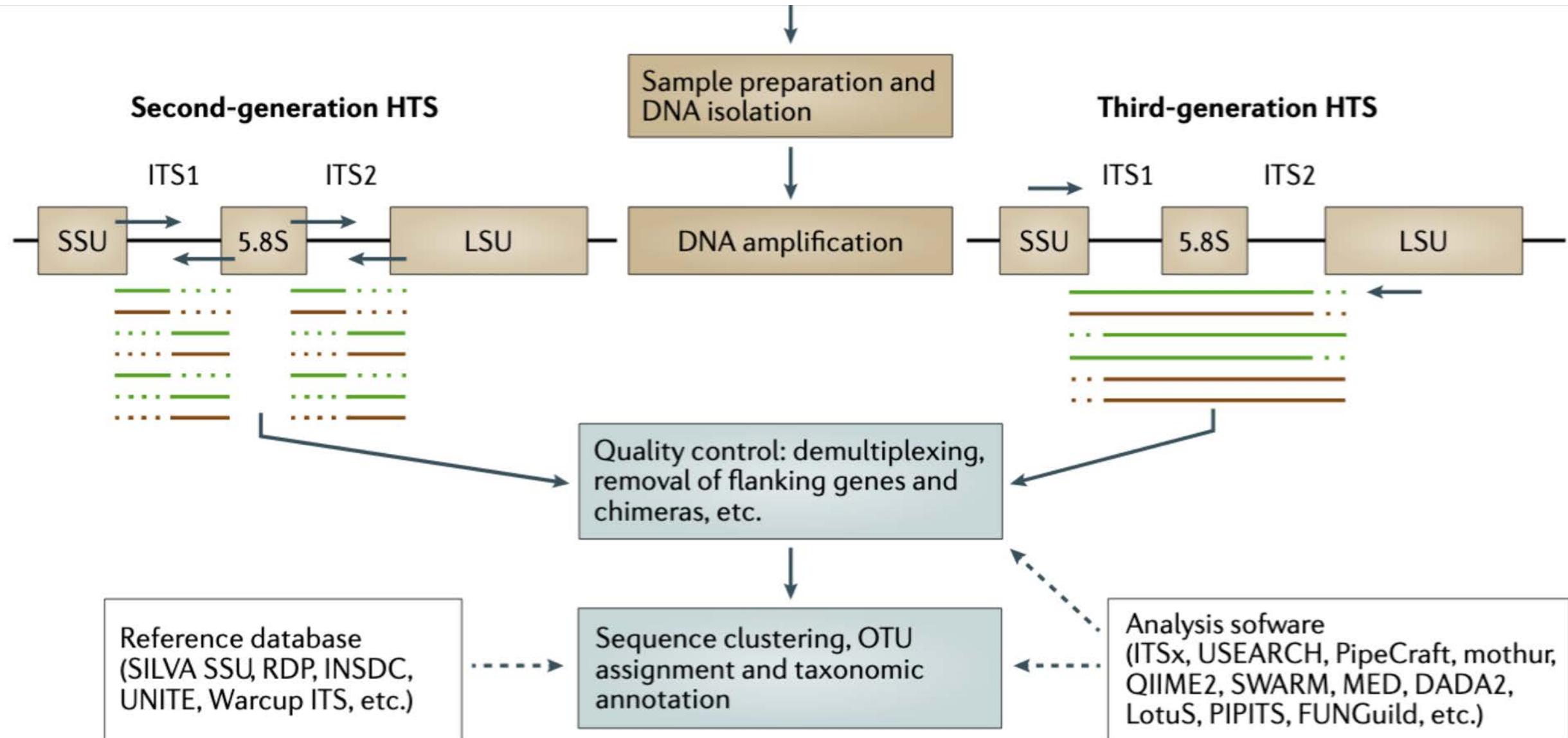
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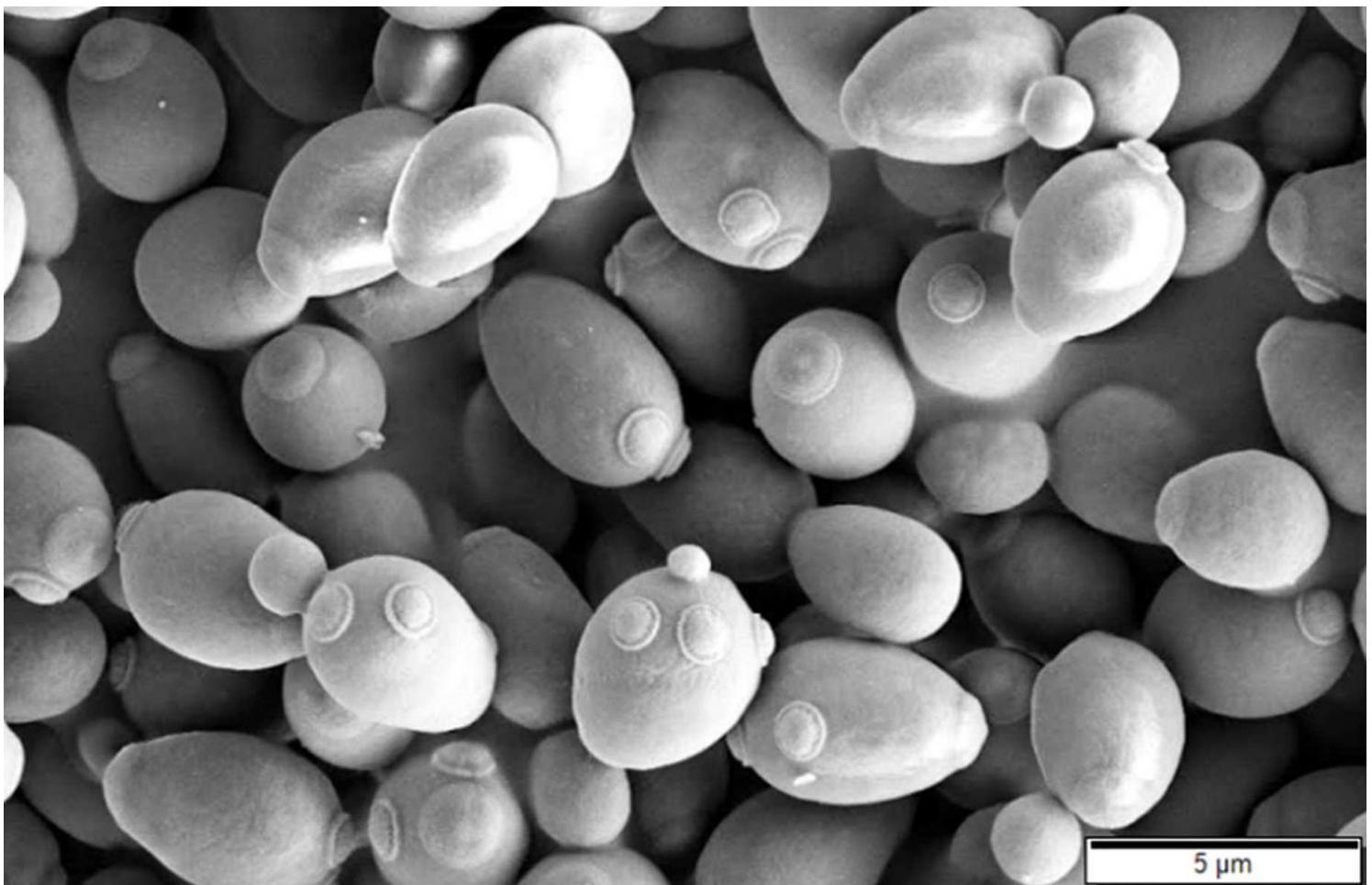
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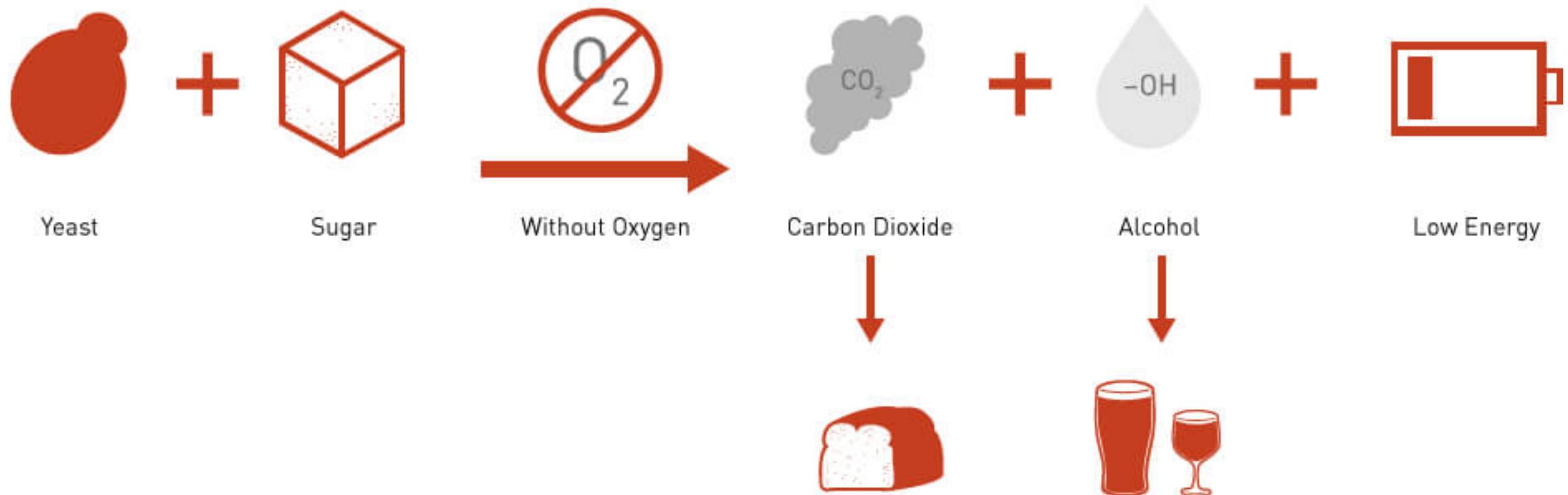
Main steps in a fungal metabarcoding project



Case studies: Origin of *Saccharomyces cerevisiae*



S. cerevisiae arguably one of the most domesticated species for its fermentation product



Revealing a 5,000-y-old beer recipe in China

Jiajing Wang^{a,b,1}, Li Liu^{a,b}, Terry Ball^c, Linjie Yu^d, Yuanqing Li^e, and Fulai Xing^f

^aStanford Archaeology Center, Stanford University, Stanford, CA 94305; ^bDepartment of East Asian Languages and Cultures, Stanford University, Stanford, CA 94305; ^cDepartment of Ancient Scripture, Brigham Young University, Provo, UT 84602; ^dZhejiang Research Institute of Chemical Industry, 310006 Hangzhou, China; ^eDepartment of Civil and Environmental Engineering, Stanford University, Stanford, CA 94305; and ^fShaanxi Provincial Institute of Archaeology, 710054 Xi'an, China

Edited by Dolores R. Piperno, Smithsonian Institution, Fairfax, VA, and approved April 26, 2016 (received for review January 27, 2016)

https://www.youtube.com/watch?time_continue=2&v=yopenv68qt5s

SAS

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'World's oldest brewery' found in cave in Israel, say researchers





COMMENTARY

Saccharomyces cerevisiae: a nomadic yeast with no niche?

Matthew R. Goddard^{1,2,*} and Duncan Greig^{3,4}



Role of social wasps in *Saccharomyces cerevisiae* ecology and evolution

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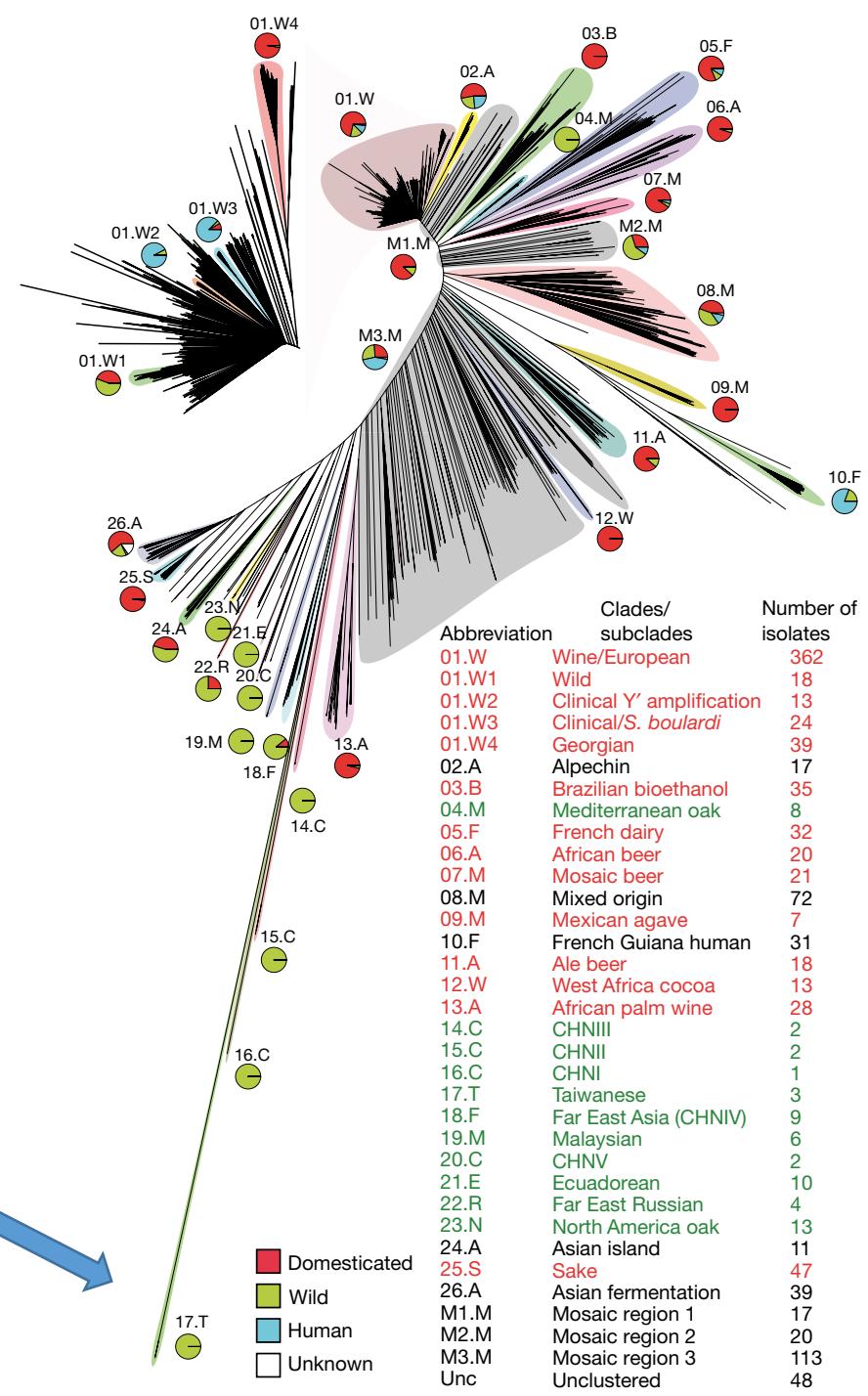
Edited by Nancy A. Moran, Yale University, West Haven, CT, and approved July 5, 2012 (received for review May 18, 2012)



Genome evolution across 1,011 *Saccharomyces cerevisiae* isolates

Jackson Peter^{1,6}, Matteo De Chiara^{2,6}, Anne Friedrich¹, Jia-Xing Yue², David Pflieger¹, Anders Bergström², Anastasie Sigwalt¹, Benjamin Barre², Kelle Freel¹, Agnès Llored², Corinne Cruaud³, Karine Labadie³, Jean-Marc Aury³, Benjamin Istace³, Kevin Lebrigand⁴, Pascal Barbry⁴, Stefan Engelen³, Arnaud Lemainque³, Patrick Wincker^{3,5,7}, Gianni Liti^{2,7,*} & Joseph Schacherer^{1,7,*}

“The Taiwanese wild lineage represents the most divergent population that has yet been described (average of 1.1% sequence divergence to non-Taiwanese strains).”



ARTICLE

DOI: 10.1038/s41467-018-05106-7

OPEN

The origin and adaptive evolution of domesticated populations of yeast from Far East Asia

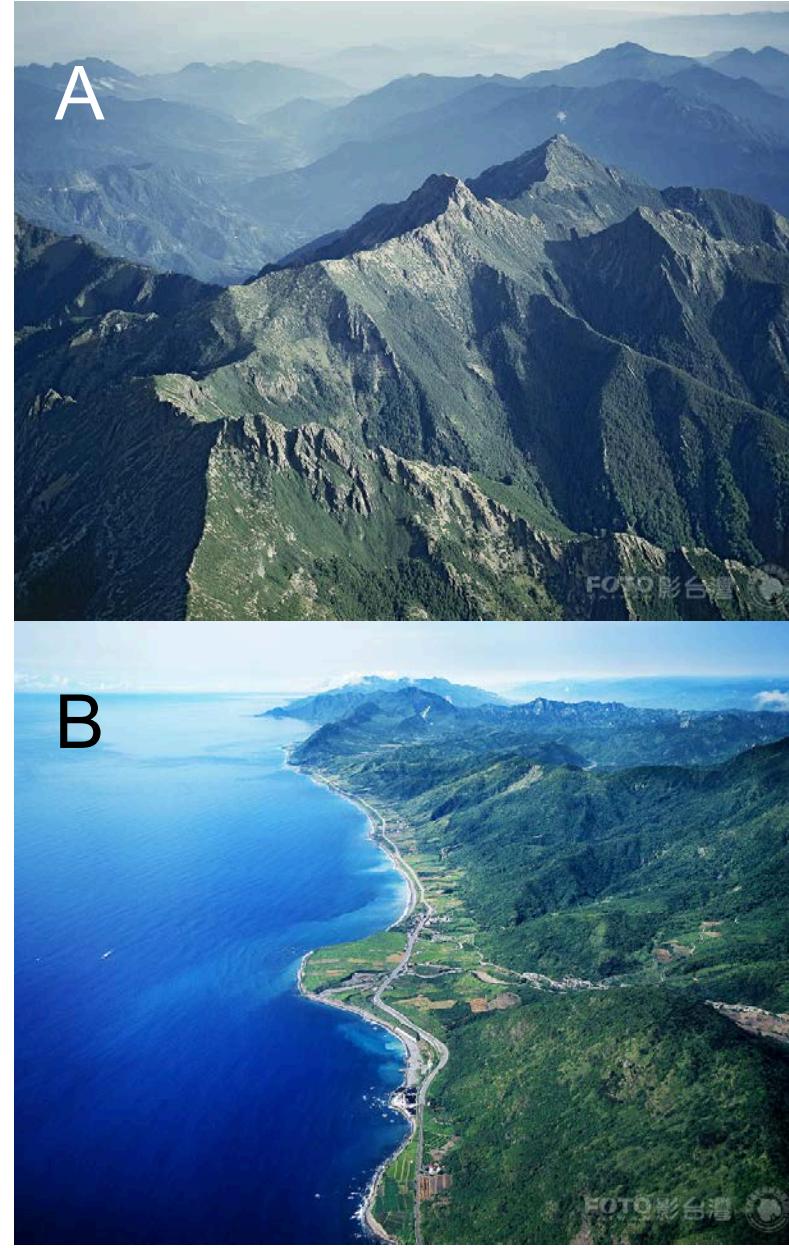
Shou-Fu Duan^{1,2}, Pei-Jie Han¹, Qi-Ming Wang¹, Wan-Qiu Liu¹, Jun-Yan Shi^{1,2}, Kuan Li¹, Xiao-Ling Zhang¹ & Feng-Yan Bai^{1,2}

a

Case studies: fungi in Taiwan

Taiwan has 9% of world's described fungal species

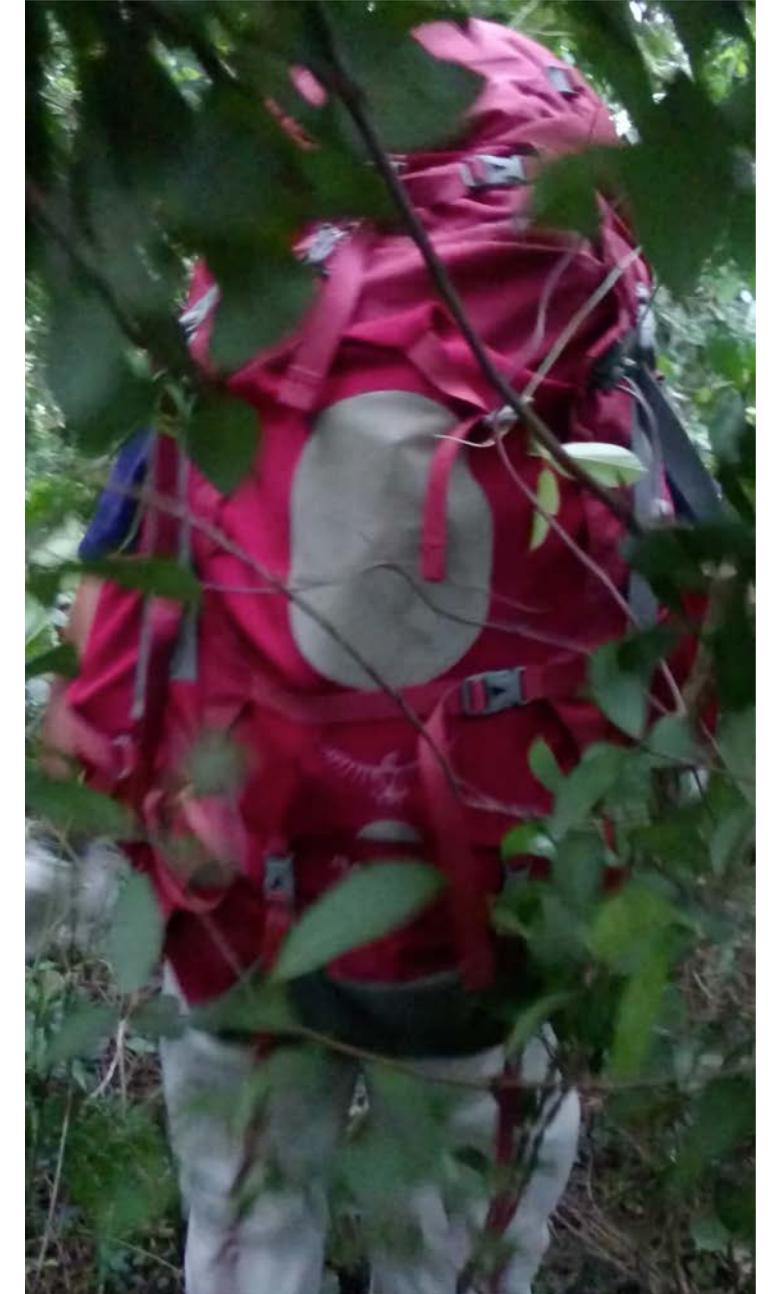




Expedition



Expedition







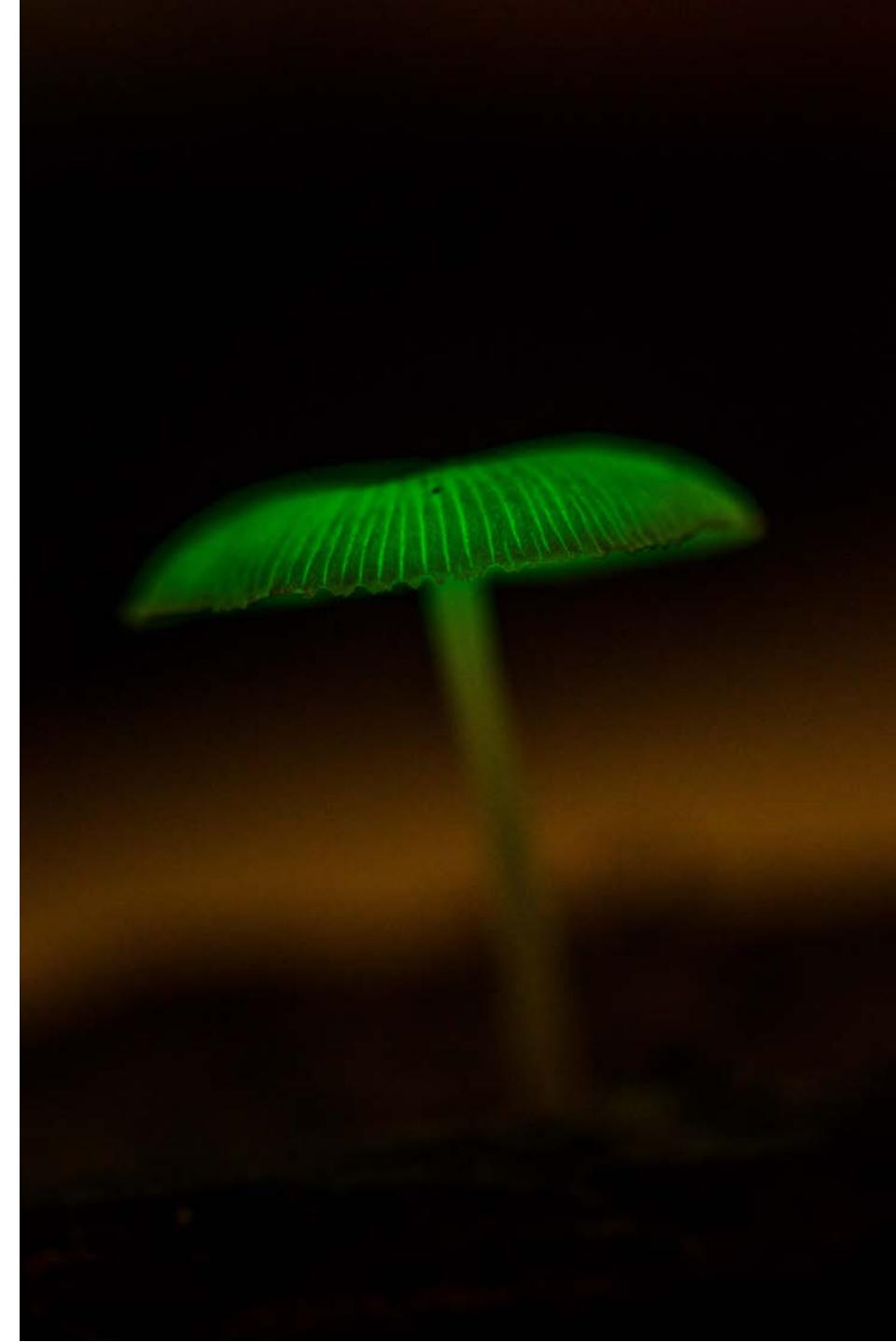


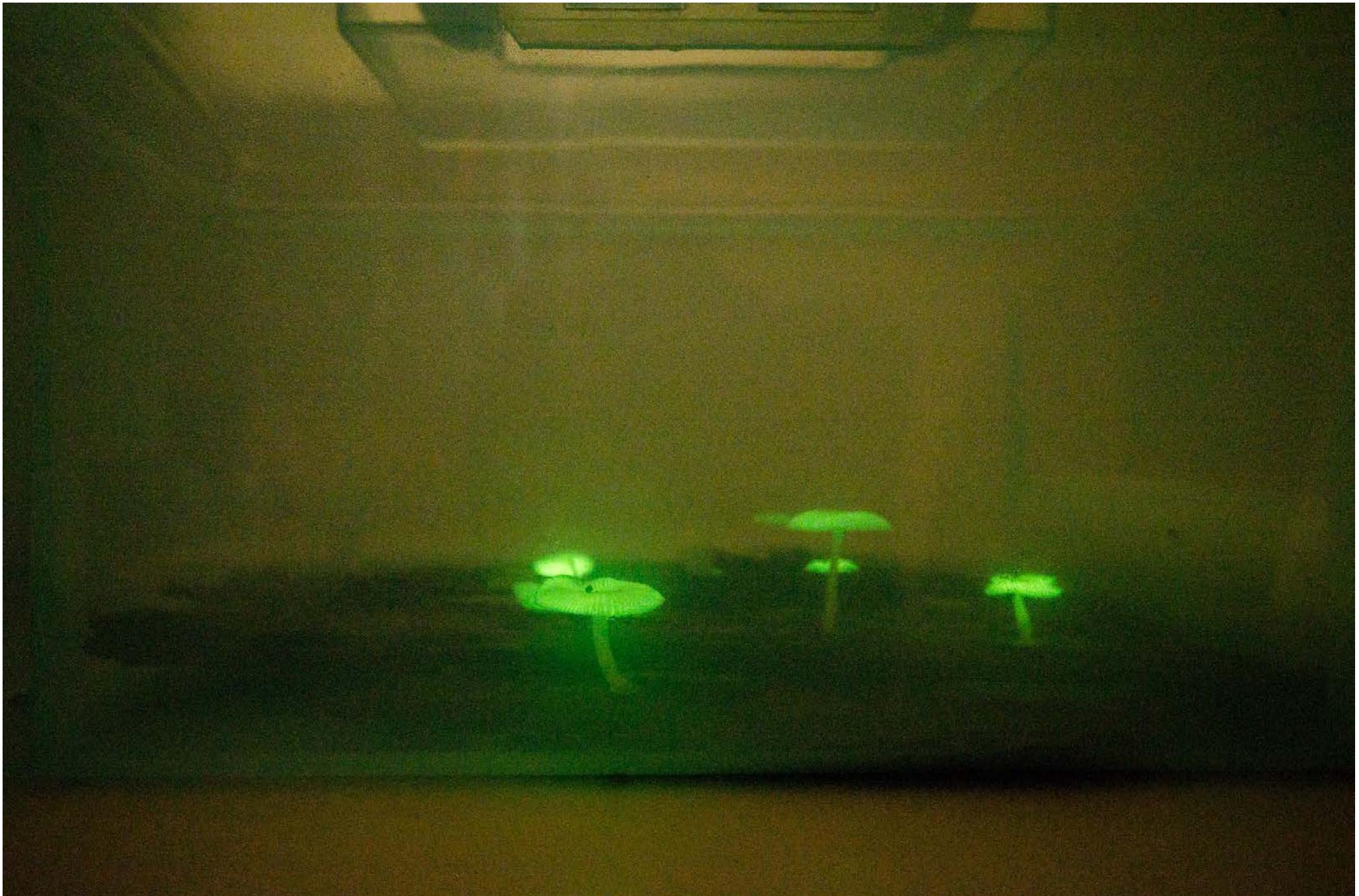






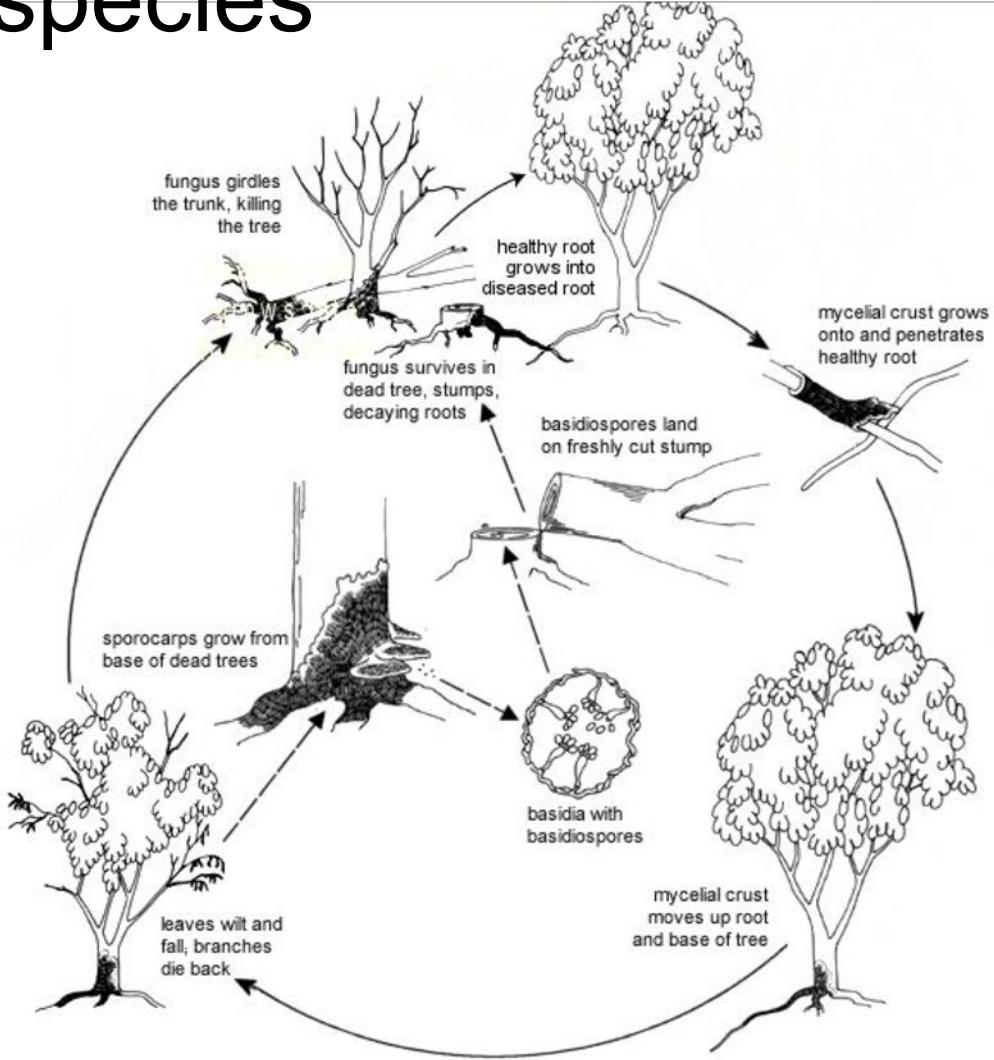






Case study : *Phellinus noxius*

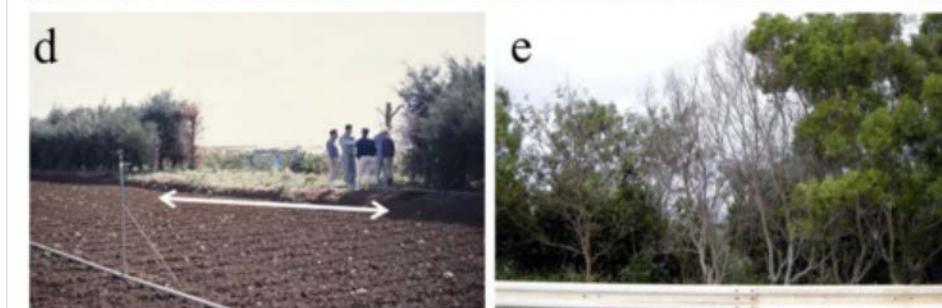
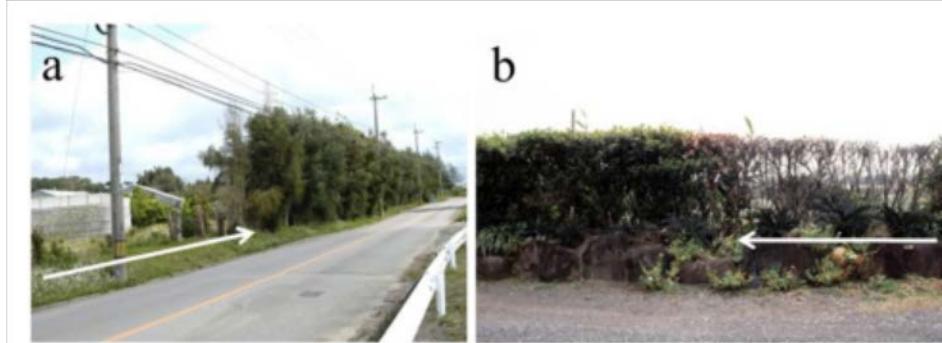
Phellinus noxius causing brown root rot in 200 + tree species



Ann et al., (2002)

Phellinus noxius 褐根病 causing brown root rot in trees

Grows in optimum temperature of 28C – an emerging issue due to climate change

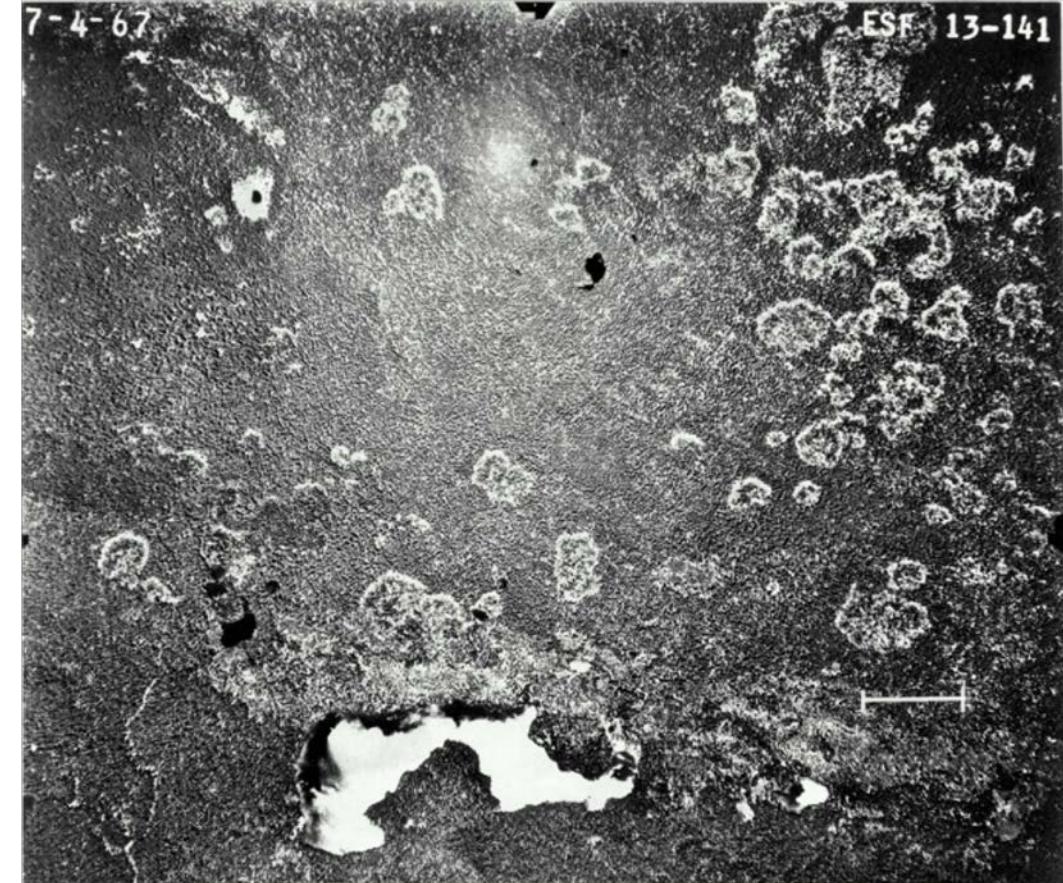


Disease foci in forests caused by *Phellinus*



Ogasawana island, Japan

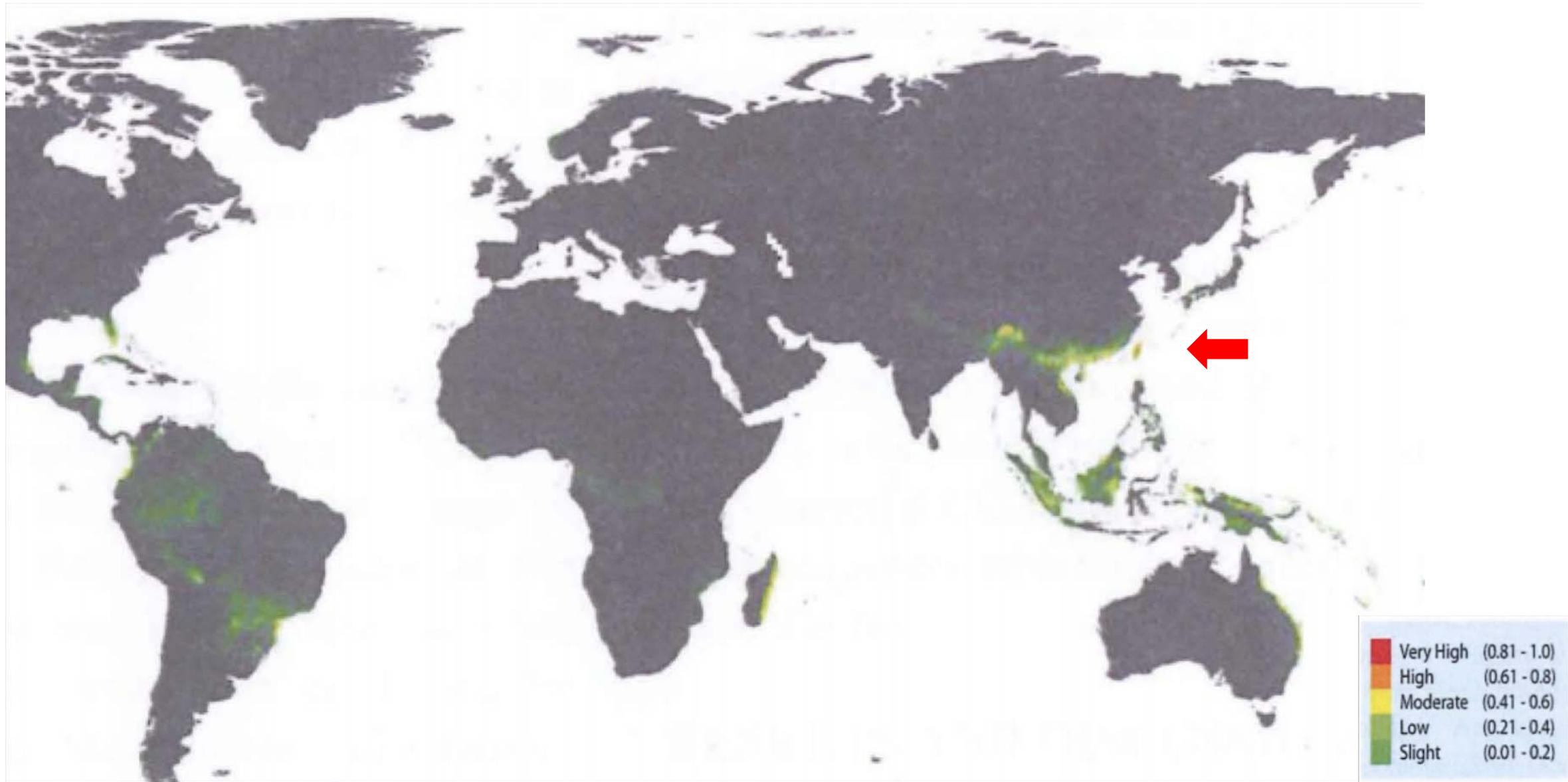
Norio et al., (2015)



Mortality centers in mountain hemlock forest at 1700 m elevation in the central Oregon Cascades.
Scale bar = 200m

Hansen 2000

Phellinus noxius distribution in the world



Transition from wood decayer to root pathogen to trunk pathogen

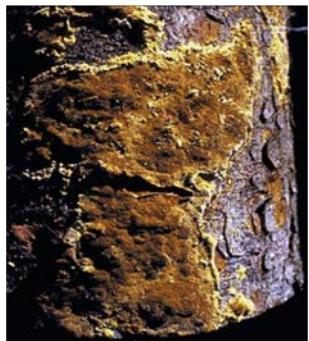
Trunk pathogen



F. mediterranea



P. pini



P. sulphurascens

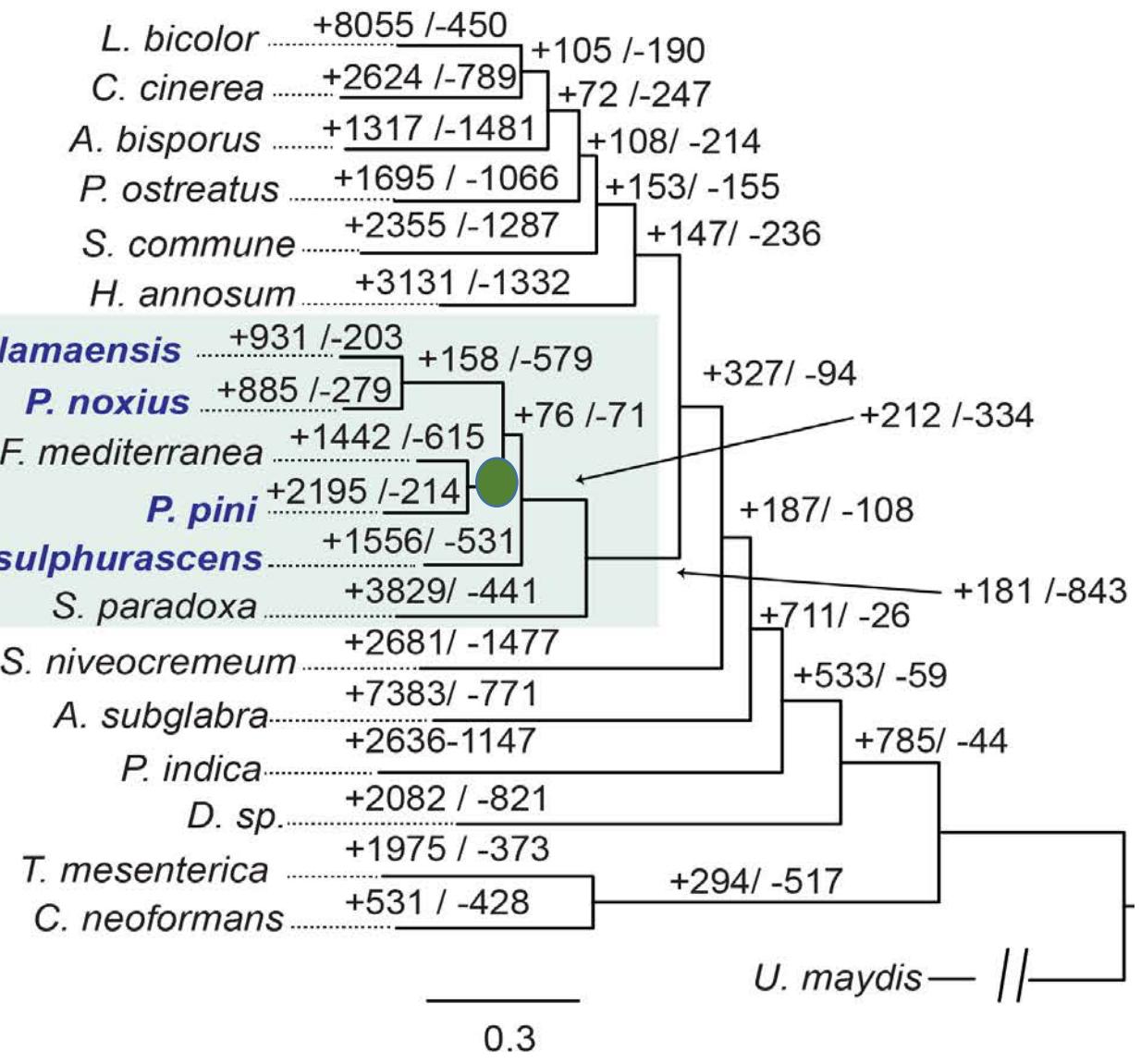


S. paradoxa

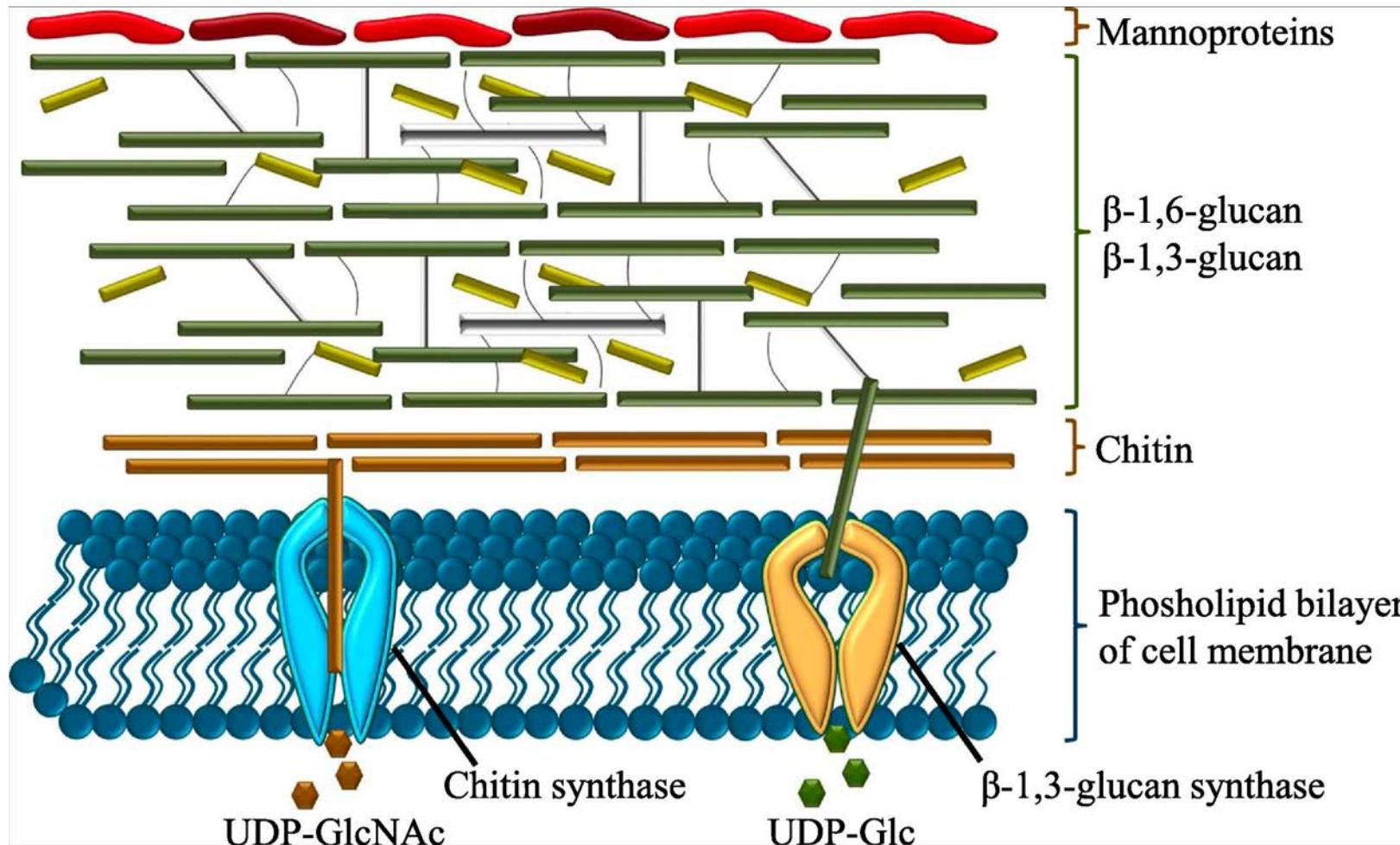


P. noxius

e



1,3-beta-glucan synthase is highly expanded in *P. noxius*

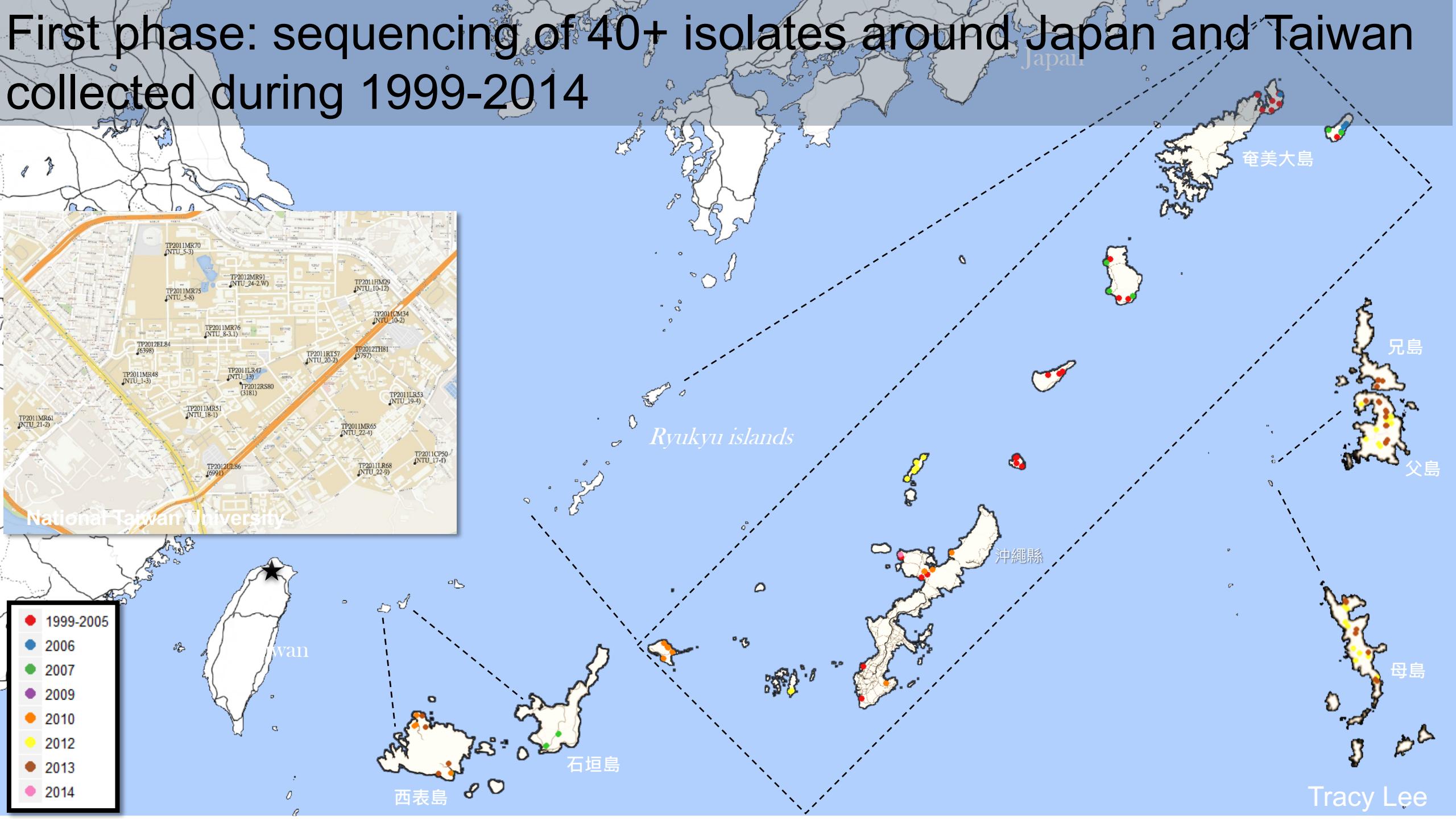


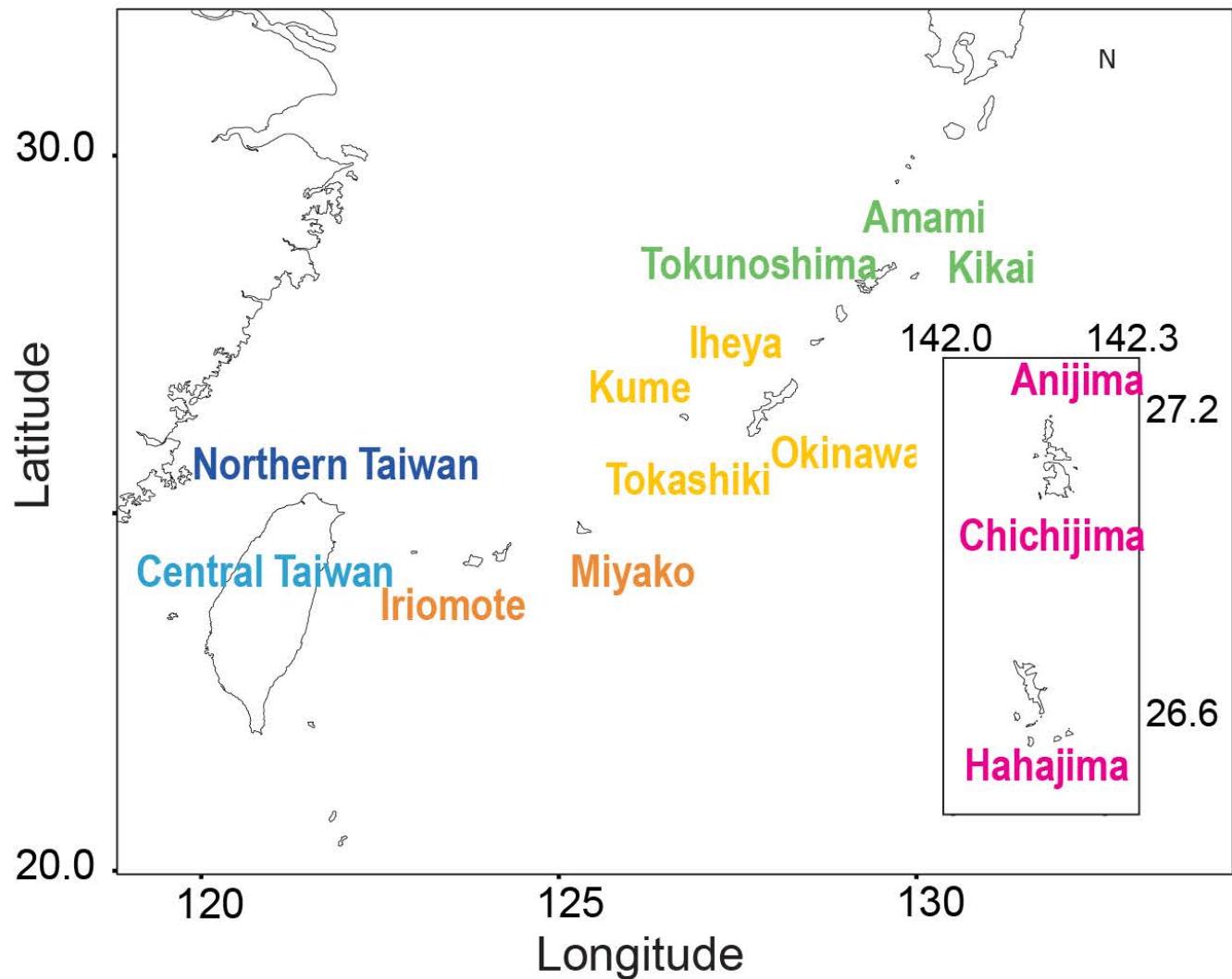
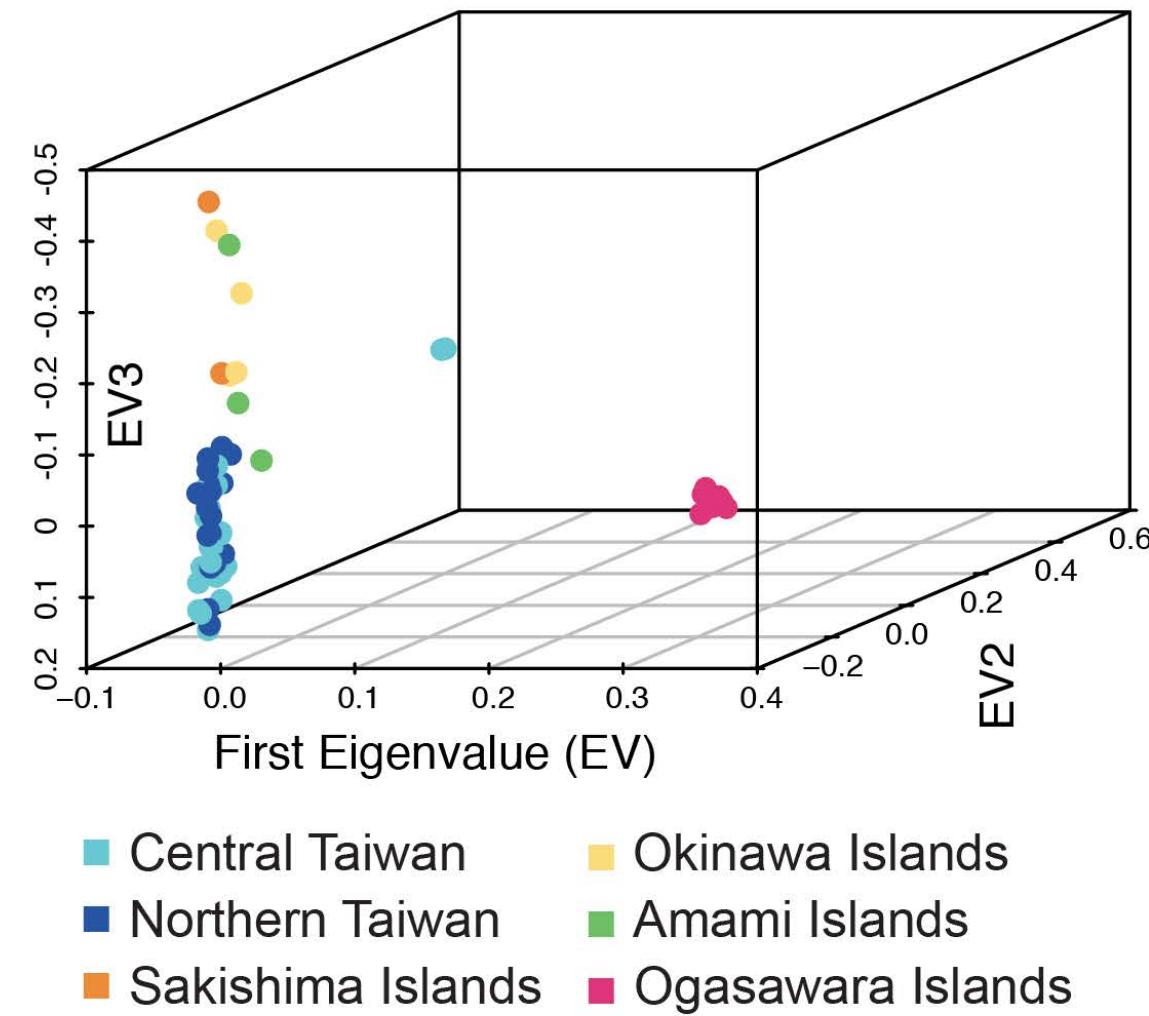
Schematic overview of fungal cell wall composition

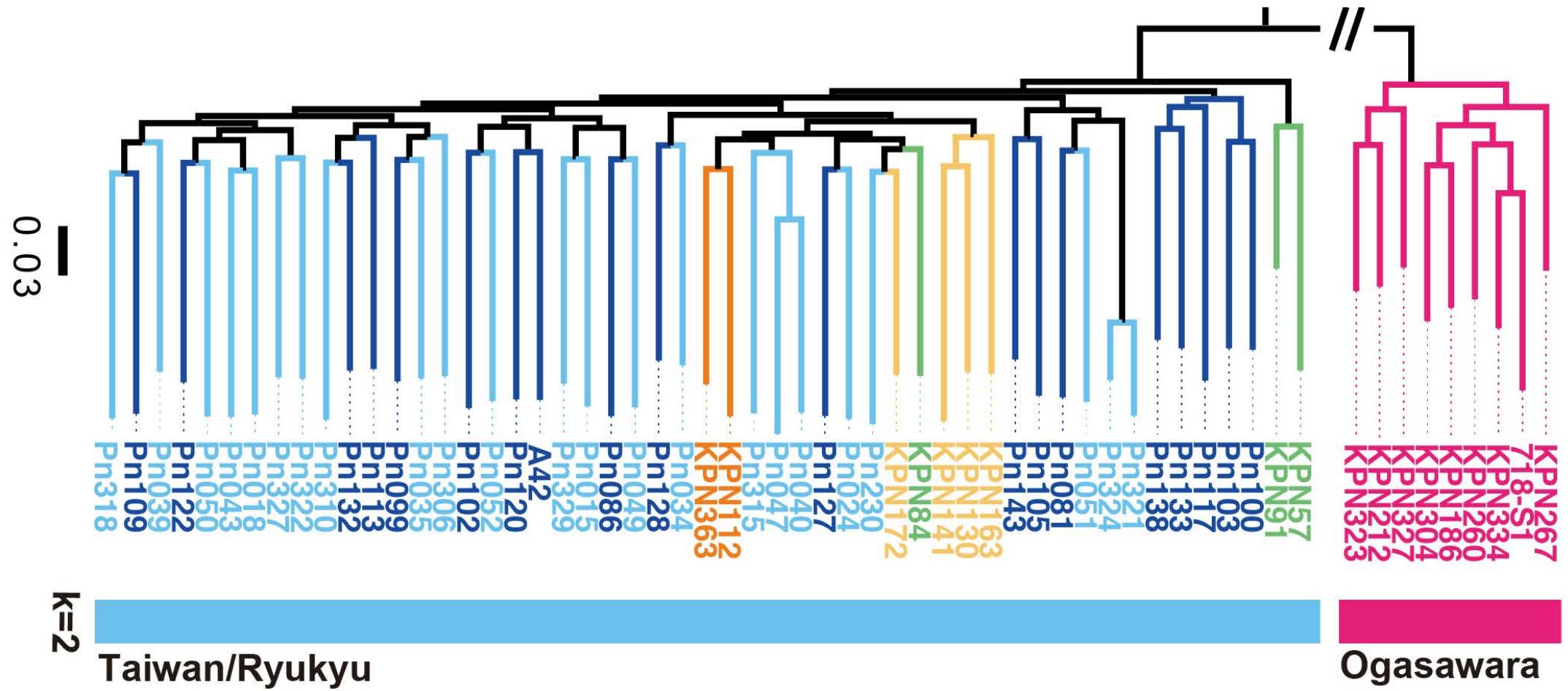
1,3-beta-glucan synthase is responsible for the formation of beta-glucan components in fungal cell wall

***P. noxius* has 14 copies, compared to an average of 1.8 copies across fungi**

First phase: sequencing of 40+ isolates around Japan and Taiwan
collected during 1999-2014



a**b**



High diversity in *P. noxi*us

Population	Sites	Segregating sites (S)	Singleton sites	$\theta\pi$ (x1,000)	θs (x1,000)	Tajima's D
Whole Chromosome						
Taiwan + Kyushu islands (n=29)	30,892,415	1,189,428	461,071	5.9	8.7	-1.2
Ogasawara islands (n=9)	28,797,609	323,021	144,718	4.1	4.2	-0.1
Synonymous sites						
Taiwan + Kyushu islands	4,715,799	408,531	140,651	14.2 (10.8 - 16.0)	19.1 (14.1 - 22.0)	-1.0 (-1.1 - -0.8)
Ogasawara islands	4,533,107	122,172	52,558	9.8 (7.6 - 10.8)	9.9 (7.7 - 11.1)	-0.08 (0.29 - 0.09)
Nonsynonymous sites						
Taiwan + Kyushu islands	9,928,193	172,035	74,244	2.5 (2.2 - 2.8)	4.0 (3.5 - 4.5)	-1.4 (-1.5 - -1.2)
Ogasawara islands	9,542,063	43,526	20,253	1.7 (1.4 - 2.1)	1.8 (1.5 - 2.2)	-0.2 (-0.4 - 0.1)

Human: 1 SNP every 1.3kb

Yeast: 1 SNP every 0.6-1.2kb

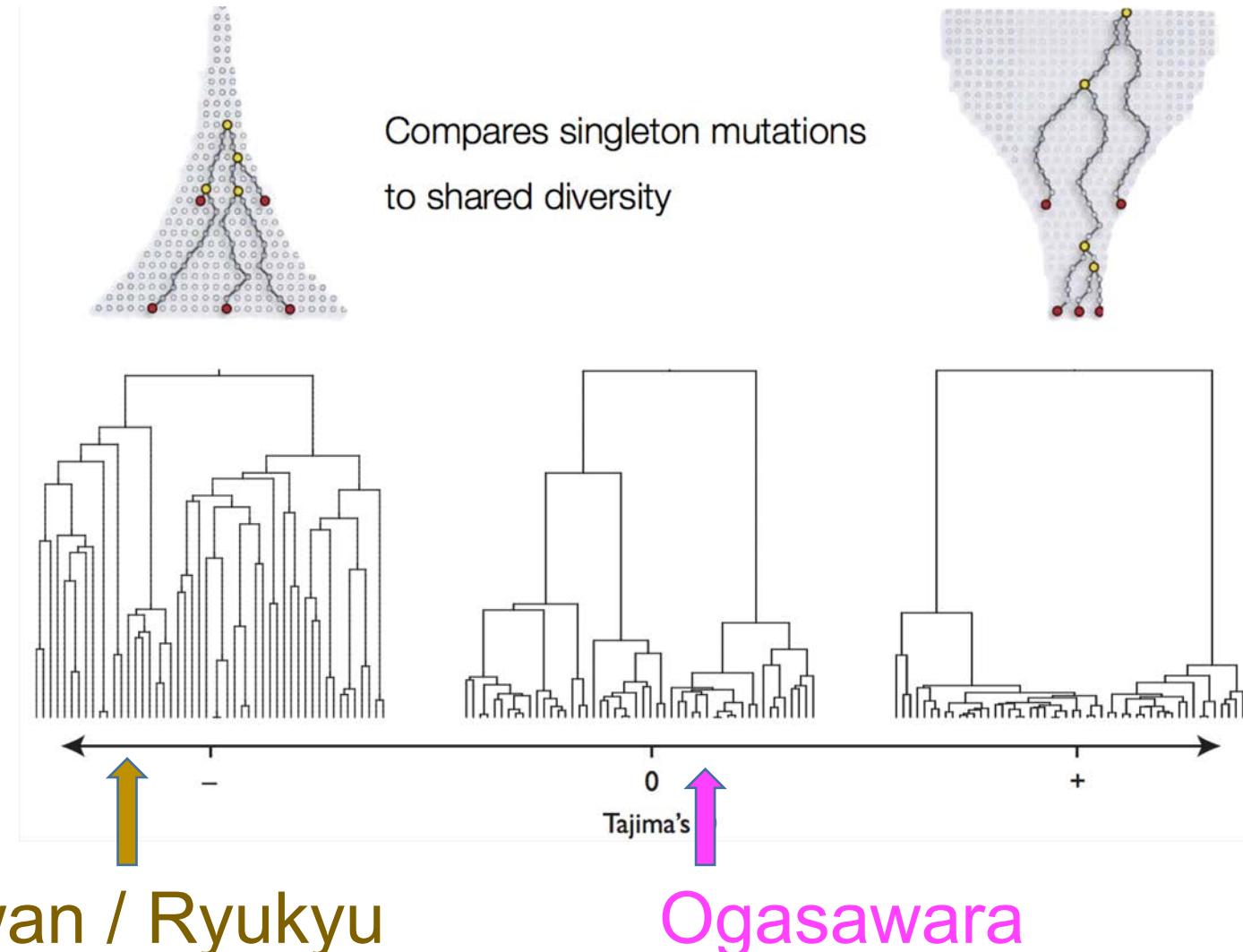
Drosophila: 1 SNP every 0.5kb

***Phellinus*: 1 SNP every 26-95bp**

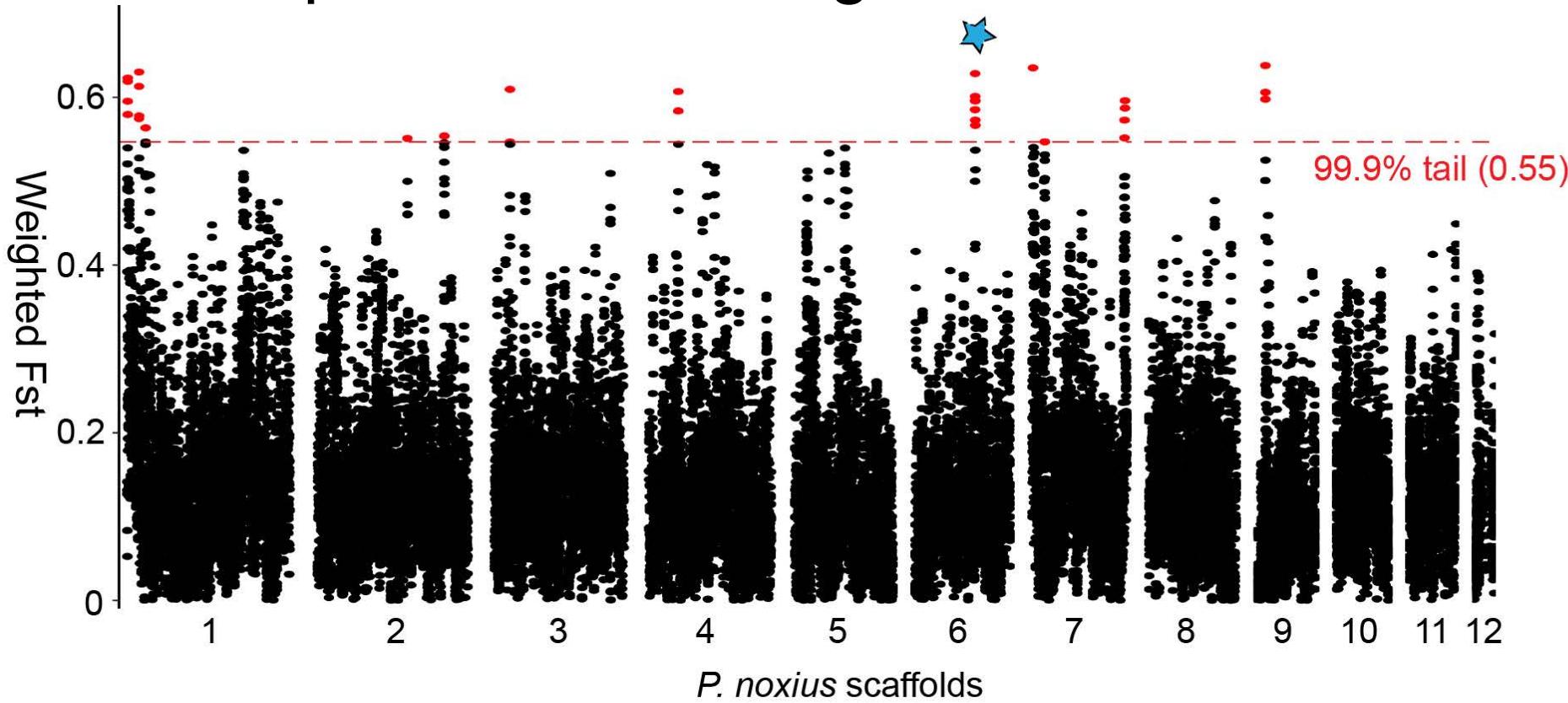
Tajima's D test if DNA is evolved under a neutral scenario (mean = 0)

A negative Tajima's D signifies an **excess of low frequency polymorphisms relative to expectation**, indicating **population size expansion** (e.g., after a bottleneck or a selective sweep) and/or purifying selection

Tajima's D statistics reveals Taiwan/Ryukyu population undergoing expansion



Population differentiated loci involved in fungal cell wall organization and plant cell wall degradation

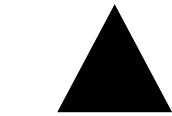


 Gene ID	Product Description	Reference of homologs
PNOK_0653900	glycosylphosphatidylinositol-anchored	Szeto <i>et al.</i> , 2007
PNOK_0654000	BEACH-domain-containing protein	Steffens <i>et al.</i> , 2015
PNOK_0654100	endo-1,4-beta xylosidase	Bray and Clark (1994)
PNOK_0654200	hypothetical protein	N/A

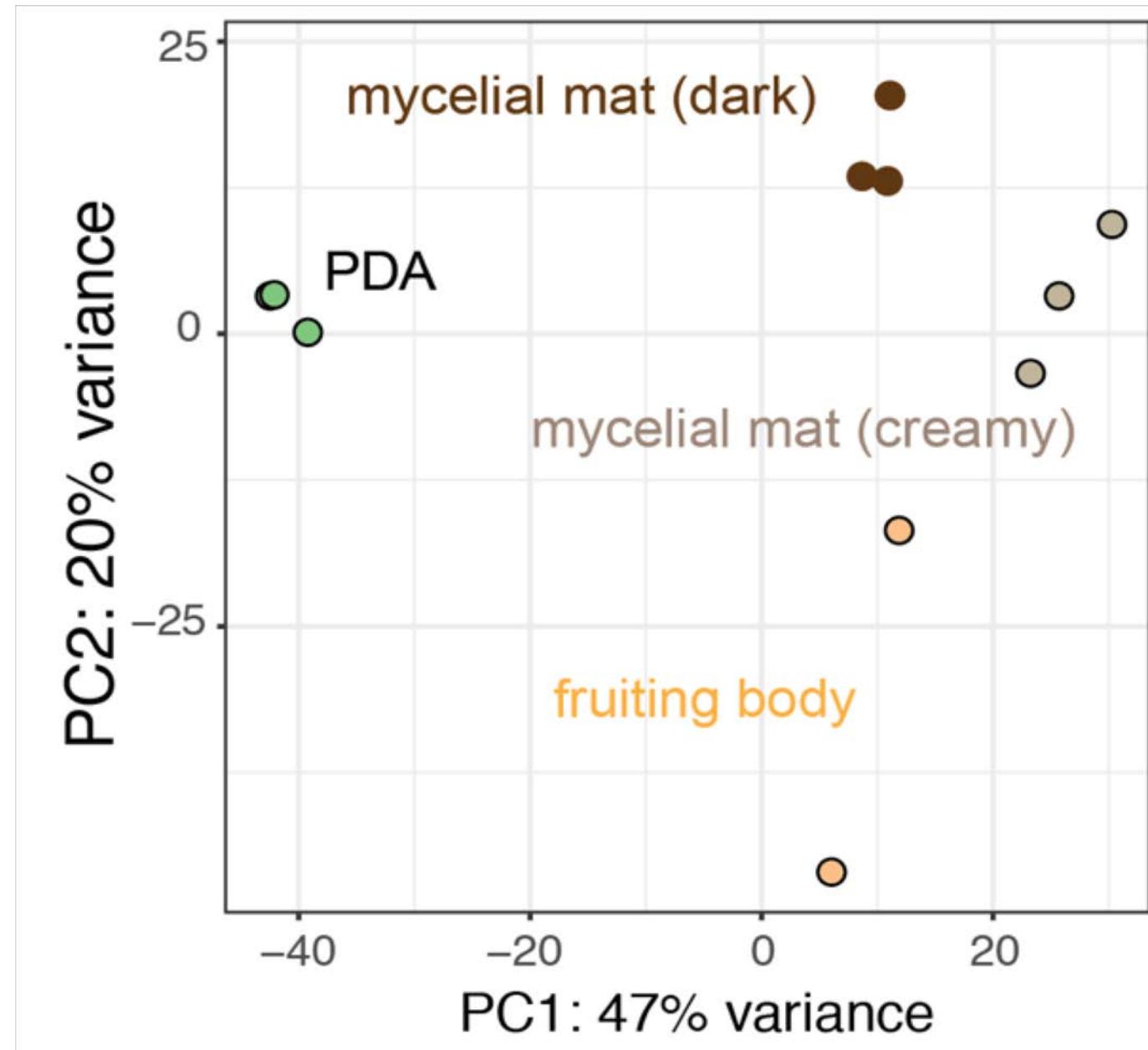
Test: RNA between different parts of infection



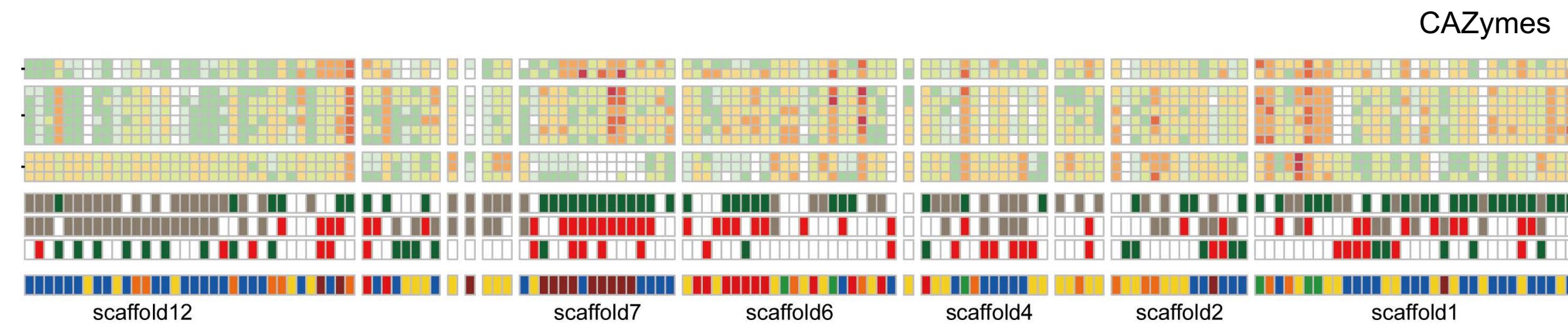
Tree 1



Tree 2



RNAseq of *in planta* samples during *P. noxius* infection



RNA between different parts of infection



Highly expressed:

Tyrosinase – key enzyme in production of melanin

Many **Hydrolases** – plant cell wall degrading enzyme

Dehydrogenase

Highly expressed in both stages:

Glycan synthetase: fungal cell wall production

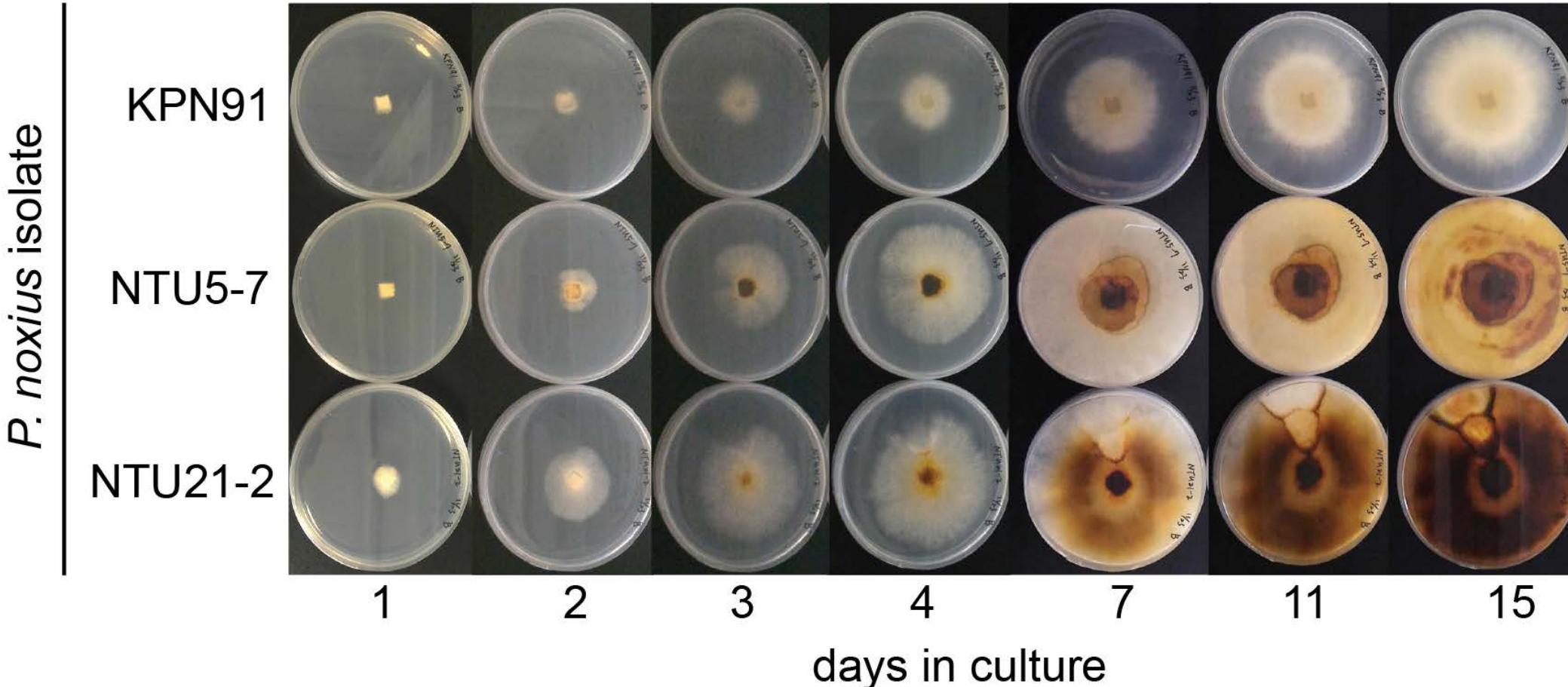
Highly expressed:

Ligninase – catalyze the breakdown of lignin, a biopolymer commonly found in the cell walls of plants

P450 – xenobiotic detoxification released from plant defense

Aspartic protease: important in the formation and germination of spores, in pathogenesis and in post-translational regulation

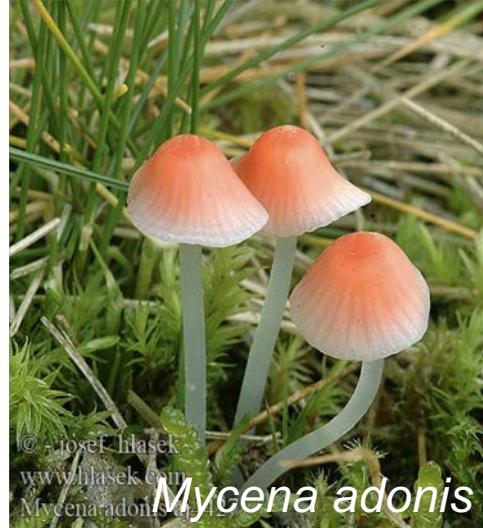
Brownness (melanin) associated with pathogenicity is different amongst isolates



Case study: Collect *Mycena* in Taiwan



Mycena interrupta



© Josef Llasek
www.llasek.com
Mycena adonis



Mycena adonis



Mycena luceptipes



Mycena leaiana

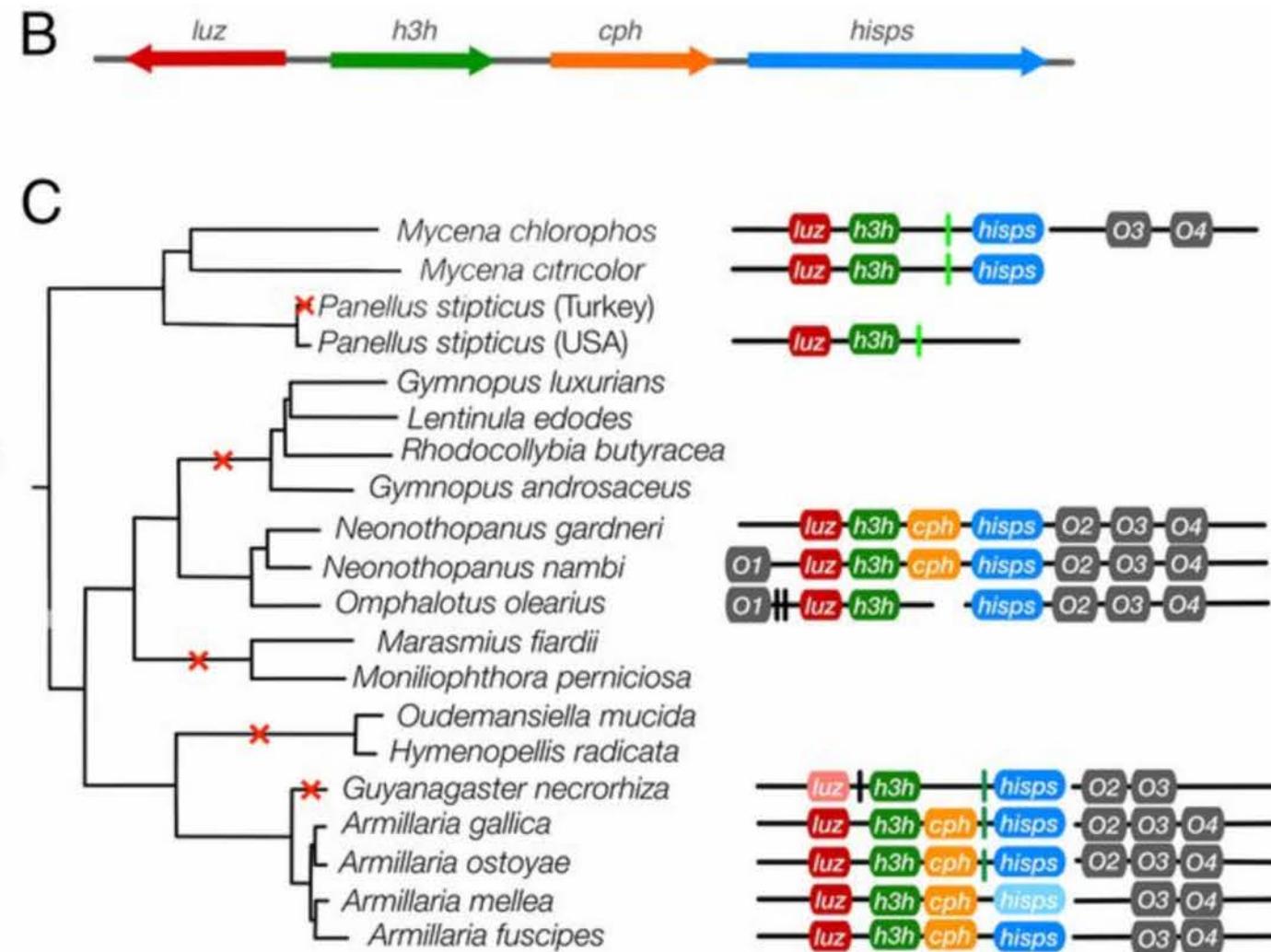
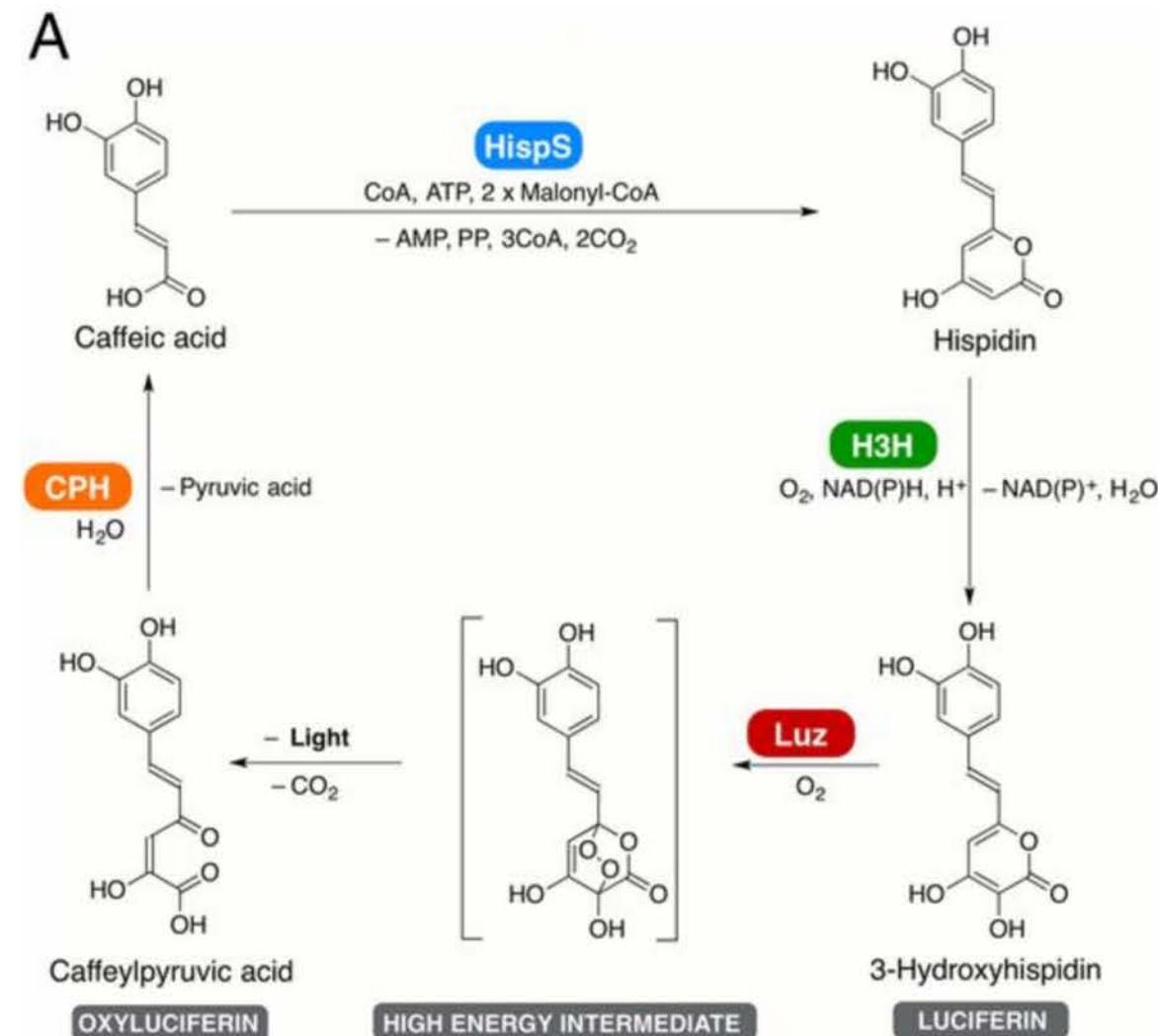
Huei mien Ke

Of the 43 species that display bioluminescence, 9 are present in Taiwan

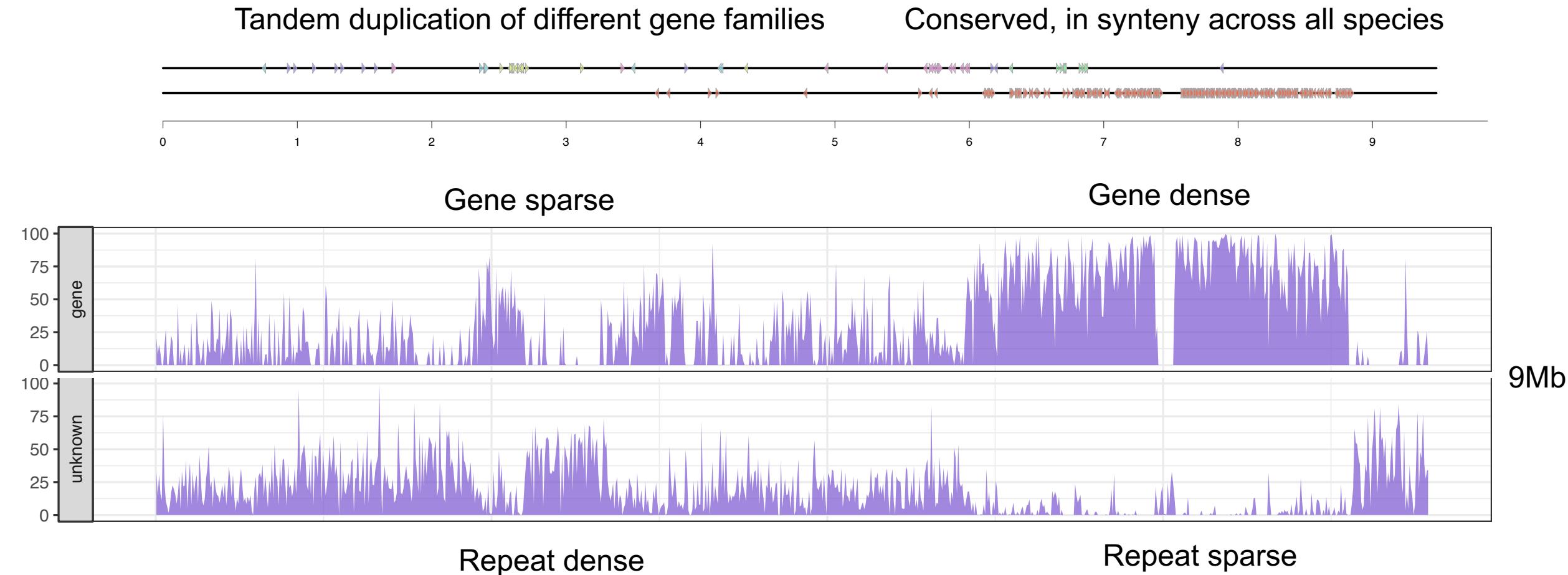


#A glowing underground network of fungi - Attenborough's Life That Glows: Preview - BBC Two
<https://www.youtube.com/watch?v=33-3UCTRZWM>

Four genes cluster constitute the Luciferin biosynthesis pathway involved in fungal bioluminescence



¹²¹ Two mode of evolution across *Mycena* genomes



- Various types of unknown repeat contribute to the expansion of genome
- Gene sparse region contain tandem duplication of various gene families
- Suggesting accumulation of repeats seems to break the synteny (regulatory) of genome allow gene families to expand

Questions and knowledge gaps

KEY UNRESOLVED QUESTIONS:

- What is the relative importance of fungal adaptation, migration and acclimatisation?
- How does climate change affect the yield of fungal spore-bearing structures?
- How does climate change affect fungal growth and activity?
- How do fungi mediate ecosystem responses to climate change?
- How do changes in the phenology of spore-bearing structure production reflect changes in activity, abundance, biomass and distribution?
- Can fungi track climate space shifts?



KEY INFORMATION GAPS:

- Long-term data
- Large-scale data
- Data from tropical, subtropical and warm temperate ecosystems
- Experimental data from fungi associated with trees, rather than seedlings
- Fungal response and effect traits
- Data from multiple simultaneous drivers of change (nitrogen deposition, carbon dioxide, ozone, UV, temperature, drought, fire)



More references

#Some nice papers

<https://www.nature.com/subjects/fungi>

Fungal Phylogenetics and Phylogenomics

<https://www.sciencedirect.com/bookseries/advances-in-genetics/vol/100/suppl/C>

The Impact of Molecular Data in Fungal Systematics

<https://www.sciencedirect.com/science/article/pii/S0065229605420029>

Genome Diversity and Evolution in the Budding Yeasts (Saccharomycotina)

<http://www.genetics.org/content/206/2/717>

Evolutionary biology through the lens of budding yeast comparative genomics

<https://www.nature.com/articles/nrg.2017.49>

Dimensions of biodiversity in the Earth mycobiome

<https://www.nature.com/articles/nrmicro.2016.59>

Evolution and genome architecture in fungal plant pathogens

<https://www.nature.com/articles/nrmicro.2017.76>