

MICROORGANISMS INCITED SPECIATION IN PLANT PATHOGENS AND EMERGENCE OF NEW PLANT DISEASES

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I. INTRODUCTION

Considering the mechanism that ensures that biodiversity is produced, speciation—the splitting of one species to two—is one of the most fundamental issues in biology. In the situations of agricultural pathogens, newly emerging human diseases, or fungal species utilized in industry and biotechnology, understanding how the 1.5 million fungal species (Hawksworth, 1991) have emerged is of basic importance and has enormous practical implications. Though much has changed since Darwin's book on the origin of species in 1859, the issue is still hotly contested. Although they are still hardly mentioned in general discussions on this topic, fungi are suitable models for studying the phenomenon of eukaryotic speciation in nature (Coyne and Orr, 2004). For starters, many fungi can be developed and mated in the lab, and mycologists have long reported various mating studies between fungal species. Second, the enormous range of life cycles and geographic distributions seen in fungi makes it possible to analyze the factors that have the greatest impact on speciation processes. Third, large species complexes containing numerous recently

divergent sibling species are known in fungus (Dettman et al., 2003), allowing research on the early stages of speciation. Understanding the demographic and ecological factors that drive their evolution will significantly broaden our knowledge about the way plant-pathogen species adapt to agricultural environments and provide new information for the management of plant diseases. Fungi are excellent models for comprehending the biological characteristics that result in new species in general, in addition to these possible applications. About 70,000 different species of fungi have been identified (Hawksworth, 1997), and many of these can infect a variety of plant hosts and cause diseases. Because pathogen biology offers an exceptional insight into how species interactions impact divergence patterns in many animals and permits the formation of precise hypotheses, these features make them ideal models for evolutionary biologists. For instance, it is anticipated that host-range expansion and host jumps will be two of the key mechanisms supporting the creation of new plant-pathogen species, given the dependence of these diseases on their host species (Broderset al., 2012). As we explore the patterns of speciation in fungi, we first discuss the issue of species definitions and species criteria before putting them in the context of the general theory as it pertains to eukaryotes. We pay special attention to elements like sympatric speciation, cospeciation, hosts changes, reproductive character displacement, and the time course of speciation that have undergone recent and noteworthy advancements.

II. SPECIES DEFINITION VS SPECIES CRITERIA

It seems important to first designate species in order to examine speciation. One could believe there is no widespread consensus over what species are given the constant introduction of new species concepts. Instead, it has been asserted that all contemporary biologists concur that species correspond to portions of evolutionary lineages that evolve apart from one another (De Queiroz, 1998). The discrepancy between a species definition (describing the type of item that constitutes a species) and species criteria (standard for determining or identifying whether individuals may be regarded members of the same species) is the root of the seemingly never-ending debate over species notions. Many supposedly "species concepts" actually match species criteria, or practical ways to identify and distinguish between species (De Queiroz, 2007). For instance, the Ecological Species Concept (ESC) highlights adaptation to a specific ecological niche, the Phylogenetic Species Concept (PSC) demonstrates nucleotide divergence, the Biological Species Concept (BSC) highlights reproductive isolation, and the Morphological Species Concept (MSC) illustrates morphological divergence. As opposed to reflecting fundamental distinctions in what constitutes a species, these criteria relate to the numerous instances throughout lineage separation and divergence. One could question why disagreements exist over the species standard we use. Such criteria cannot be used universally for three basic reasons: There are several modes of speciation that can take place, and during these modes the phenomena used for species recognition do not always appear in the same chronological order. In addition, some characteristics of some organisms make it difficult to apply some criteria. Speciation is a temporally extended process, but one that differs greatly in pace among different types of organisms. Consider the BSC, the most widely used but most problematic species criterion. The ability to interbreed defines the infraspecies level in the eyes of BSC proponents, and "Biological Species" are intersterile groups (Mayr, 1942). Although reproductive isolation is the basis of this criterion, speciation occurs at many different phases. Intersterility can occur early or late in the process of speciation and can be a crucial stage (in sympatric speciation), or it can simply be a byproduct of genetic divergence (in allopatric speciation). This depends

on the method of speciation. Obviously, in the first scenario (sympatric speciation), the BSC will be most helpful, whereas in the second scenario, species criteria based on genetic marker evidence for lack of gene flow will be more discriminating. The point at which the process has become irreversible is known as intersterility, but it may take a very long time to get there. The MSC has traditionally been the most popular species criterion for fungus. However, employing the BSC (Anderson and Ullrich, 1978) or the GCPSR (Genealogical Concordance Phylogenetic Species Recognition), a development of the PSC, several cryptic species have been found inside morphological species. The later species criterion makes advantage of the phylogenetic concordance of numerous unrelated genes to show that there has been little genetic exchange and that lineages have evolved independently. Thus, species that are difficult to distinguish using other species criteria because they lack morphological features or have insufficient prezygotic isolation might be found. The GCPSR criterion, which is currently the most prevalent in the fungal kingdom, has proven to be incredibly helpful in fungi since it is frequently more precisely discriminating than the other criteria or more practical (for example, for species that we are not able to cross).

III. HOW TO STUDY SPECIATION IN PLANT PATHOGENS

The presence of distinctive RIMs marks the end of speciation. Understanding what biological characteristics restrict gene flow is therefore crucial to understanding how species arise. Despite the fact that study in plant pathology is not typically referred to as speciation research, a number of strategies have been employed to examine the biological underpinnings of reproductive isolation between plant-pathogen species. We categorize these research into two groups, with the classical studies being those that have shown RIMs between species. The second group, referred to as genomic studies, includes genome-scale investigations that pinpoint genomic elements related to reproductive isolation or interspecies variations. Allopatric speciation, sympatric speciation, and ecological speciation are examples of classical research, whereas hybridization-based speciation and chromosomal speciation are examples of genomic studies. Below is a discussion of each of these research (Restrepoetal., 2014).

- 1. Allopatric Speciation:** Research on how new species develop through natural processes is still very much underway. Because extrinsic geographic constraints represented clear obstacles to gene flow, it has long been thought that species originate primarily by means of allopatric divergence (Mayr, 1963). Because eukaryotic microbes have long been thought to have worldwide geographic ranges (ubiquitous dispersal theory; Finlay, 2002), at least for those that aren't reliant on a host having a constrained range, fungi could appear as exceptions. This was especially true for fungal diseases that are airborne since their spores can travel extremely far. However, given that the cryptic species represent non-overlapping areas divided by physical barriers, many of the complexes of sister species recently discovered using the GCPSR criterion look similar to allopatric divergence (Taylor et al., 2006). Recent examples include the discovery of cryptic species among *Neurospora crassa*, a morphological species, using a multiple gene genealogies technique (Dettman et al., 2003). One phylogenetic species was found in the Congo, another in the Caribbean and Africa (but not Congo), and a third was confined to India. Their non-overlapping geographic ranges indicated allopatric speciation. *Saccharomyces paradoxus*, a close relative of *Saccharomyces cerevisiae* found in temperate forests in the northern hemisphere, was shown to be formed of two separate genetic groups, A and B,

as demonstrated in yeasts by Kuehne et al. (2007) using a similar multiple gene genealogies approach. All of the isolates from group B were found in North America, but the bulk of those from group A came from Eurasia, suggesting that these early species may have evolved on distinct continents. Another illustration is provided by *Fusarium graminearum*, a fungus that causes scab on wheat and barley and was formerly thought to be a panmictic species with a wide distribution. But according to recent research, there are at least nine phylogenetically distinct species that are geographically isolated (O'Donnell et al., 2004). One was only found in Central America, four were obviously unique to South America, one was found in India, and one was found in Australia (O'Donnell et al., 2004). Basidiomycetes also contain examples (Table 1), such as *Armillaria mellea*, where both North American and **European strains have been identified.**

Table 1: Speciation Cases Reported to be Allopatric

Sl No.	Species	Speciation Mode	Comments
1	<i>Ceratocystis fimbriata</i>	Allopatric	Fungi and hosts show disjoint ranges
2	<i>Phytophthora nicotiana</i>	Allopatric	Speciation occurred after an allopatric period
3	<i>Venturiainaequalis</i> ecotypes	Allopatric	Wide geographic divergence
4	<i>Fusarium nepalensis</i>	Allopatric	Geographic range of all species does not overlap
5	<i>Fusarium graminearum</i>	Allopatric	Geographic range of all species does not overlap
6	<i>Pyrenophora tritici-repentis</i>	Allopatric	Glacial refuges may have provided conditions for speciation
7	<i>Microbotrym lychnidis-dioicae</i>	Allopatric	Very little or no recent gene flow was detected

- 2. Sympatric Speciation:** Compelling evidence for the sympatric divergence is extremely difficult to provide, because excluding a past period of allopatry is almost always impossible (Coyne and Orr, 2004). Evidence consistent with sympatric divergence of fungal populations driven by parasitic adaptation to different hosts has however been reported. An example is provided by *Ascochyta* pathogens, where recent multilocus phylogenetic analyses of a worldwide sample of *Ascochyta* fungi causing blights of chickpea, faba bean, lentil, and pea have revealed that fungi causing disease on each of these hosts form distinct species (Peever, 2007). Experimental inoculations demonstrated that infection was highly host-specific, yet in vitro crosses showed that the species were completely interfertile. The host specificity of these fungi may therefore constitute a strong reproductive barrier, and the sole one (Peever, 2007), following a mechanism of sympatric divergence by host usage. The coexistence in sympatry of interfertile populations specialized on different hosts that remain reproductively isolated cannot indeed be explained currently by models other than the reduced viability of immigrants. This mechanism seems to be able to maintain the species differentiated in sympatry and could similarly have created the divergence in sympatry. It is however difficult to exclude

a period of allopatry in the past that would have facilitated specialization, i.e., the accumulation of different alleles beneficial on alternate hosts. An elegant way to demonstrate the sympatric occurrence of speciation is to show that gene flow has occurred after initial divergence (Wu and Ting, 2004). This approach is very promising and has been used so far in fungi only on *Mycosphaerellagraminicola*, showing that this wheat pathogen arose recently, most probably during wheat domestication in the fertile crescent, by sympatric differentiation from *Mycosphaerella* species pathogens of natural grasses (Bhat *et al.*, 2009). Table 2 shows some more examples.

Table 2: Speciation Cases Reported to be Sympatric

S. No.	Species	Speciation Mode	Comments
1	<i>Botrytis cineria</i>	Sympatric	Ecological factors favoured speciation
2	<i>Didymellarabiei</i>	Sympatric	Speciation occurred geographic proximity
3	<i>Mycosphaerellagraminicola</i>	Sympatric	Coalescent analysis show little or no gene flow during the divergence process
4	<i>Phytophthorainfestans</i>	Sympatric	No change in geographic range since speciation
5	<i>Botrytis cineria ecotypes</i>	Sympatric	No geographic barriers separated pathogen populations
6	<i>Rhizoctoniasolani</i>	Sympatric	Species are currently sympatric in their geographic range
7	<i>Phytophthora mirabilis</i>	Sympatric	No geographic barriers separated pathogen populations

IV. NATURE OF REPRODUCTIVE ISOLATION

The fundamental requirement for speciation in sexually reproducing organisms is the restriction of gene exchange between emerging species due to the emergence of barriers to reproduction. These barriers are classified as prezygotic and postzygotic, depending on whether they operate before or after fertilization. However, in fungi with extended dikaryotic stages, the term "postzygotic" can be unclear due to the delayed nuclear fusion. Thus, for fungi, we'll use "pre-mating" and "post-mating" to describe barriers before or after cell fusion. Initial isolation can take various forms. In organisms relying on biotic vectors, specialized vectors can hinder contact between populations, even if they are close, resulting in ecological isolation. For example, the *Microbotryum violaceum* complex involves distinct insect vectors for different host species, limiting mating opportunities between strains from separate plants, though not completely. Ecological isolation can also arise within habitats (parasite hosts) due to specialization, preventing mating even within the same environment. Differences in reproductive timing, known as allochrony, can also foster isolation. For instance, sister species like *Saccharomyces cerevisiae* and *S. paradoxus* exhibit distinct growth kinetics, enabling intraspecific breeding before or after interacting with the other species. This reduces interspecific mating without invoking incompatibility. Self-pollination, seen in plants, can

effectively curb interspecific mating. In the anther-killing fungus *M. violaceum*, self-pollination acts as a reproductive barrier. Assortative mating, based on mate recognition, is pivotal in isolating Homobasidiomycota. Mycelia of the same species predominantly form clamp connections, indicating mate preference. Postmating isolation involves barriers like hybrid inviability and sterility, stemming from incipient species divergence. After mating, unsuitable hybrids result from heterospecific crosses. Hybrids may be inviable or sterile due to genetic incompatibility, known as Dobzhansky–Muller incompatibility. This intrinsic isolation is evident in failed *in vitro* outcrossing experiments. For example, *Microbotryum* species' heterospecific crosses yield fewer viable mycelia, and *Neurospora* species' crosses lead to abnormal perithecia or ascospores. Postmating isolation can also hinge on environmental factors. Hybrids may thrive in benign settings, like *in vitro* conditions, but struggle in the wild. Hybrids with intermediate traits between parents can be poor competitors in both parental environments. Such ecological barriers are scarcely studied in fungi. In the *Microbotryum violaceum* complex, hybrids fare well on one host but not on another, demonstrating environment-dependent viability. Though mycologists have extensively studied *in vitro* premating and postmating barriers, ecological barriers are underexplored in fungi. Investigating reproductive isolation in fungi, both in the lab and nature, could shed light on how different barriers reduce gene flow between sibling species and offer insights into the timing of barrier emergence during speciation

- 1. Speciation by Hybridization:** Various fungi exhibit incomplete sterility, facilitating quicker hybridization. Hybrid speciation is categorized by the ploidy level: Allopolyploid speciation occurs when the hybrid's chromosome count matches the parent species, while heterodiploid or homoploid hybrids share the same ploidy as parents. Allopolyploids often possess higher ploidy than parental lineages, yet their karyotypes might not fully complement both parent genomes due to chromosomal loss, potentially leading to the underestimation of ancient polyploid events. Recently, allopolyploid hybrids have been found in *Botrytis allii*, causing gray mold neck rot in onions and garlic. The prevalence of hybrids in certain taxa suggests their potential selective advantage over parent species. Aneuploidy provides immediate isolation and creates a new ecological niche through triploidy in backcrossing. Autopolyploid speciation, on the other hand, involves hybrids with the same ploidy level and wide heterozygosity as their parents. Unlike allopolyploids, autopolyploid hybrids compete not only with parents but also with backcrossed individuals, resulting in stable allodiploid species, unlike polyploids. Homoploid speciation is exemplified by Rust *Melampsora columbiana*, resulting from the cross between *P.americana* parasite *M. medusa* and *P. trichocarpa* parasite *M. occidentalis*. This hybrid emerged in 1997, when rust-resistant poplar hybrids were cultivated in California, providing the homoploid hybrid with a new ecological niche on a new host. The question of why numerous loci remain genuinely heterozygous despite the potential for F1 hybrid recombination arises. This could be due to selection capitalizing on simultaneous heterozygosity at multiple loci. Intriguingly, recent focus on gene expression in hybrids offers a plausible mechanism for this advantage.
- 2. Asexual Fungi:** The challenges of speciation in asexual fungi markedly differ from those in sexual organisms. Establishing discrete species identities in asexual organisms, which lack the allele separation seen in sexual reproduction, presents a theoretical quandary. A single gene's intense selection can exert genome-wide effects, potentially leading to the emergence of new "species" through the rise of adaptive alleles tailored to novel

ecological niches. The conundrum lies in comprehending why distinct entities, definable as species, emerge rather than observing a continuous range of phenotypic/genotypic variations. Asexual organisms appear to form isolated entities even without the mingling gene flow, with theories explaining their existence encompassing factors like ecological niches, stochastic processes involving intermediate genotype/phenotype extinctions (Coyne and Orr, 2004), or the transition from sexual to asexual modes resulting in species emergence. A case in point is the *Magnaporthe grisea* complex, comprising numerous strictly asexual and host-specific variants. Notably, within this complex, a species named *Magnaporthe oryzae*—an important rice pathogen—recently emerged and played a potential role in rice domestication. Rice, barnyard grass, and finger millet exhibit distinct asexual modes and specialize as hosts. The model within the *M. oryzae* complex posits that asexual parasitic fungi's capacity to infect new hosts facilitates easy speciation due to the absence of recombination hindrance. Fungi, with their diverse reproductive modes, serve as ideal subjects for testing varied hypotheses regarding the nature of non-recombinant organisms. Nevertheless, in select asexual organisms, interconnections between individuals can arise through somatic recombination, somewhat analogous to the mating process in sexual counterparts. Mycelial fusion among genetically diverse populations is regulated by complex nutrient dynamics, yielding heterokaryosis. Nuclei and organelle exchange can induce parasexual behavior, yielding long-term changes through chromosome segregation and meiotic recombination. Fungi featuring somatic recombination, such as *Aspergillus flavus*, display vegetative compatibility groups (VCGs) that essentially establish connections between different species. This phenomenon underscores the concept of VCGs acting as bridges, not only between entities but also between diverse species.

V. WHICH FACTORS USUALLY RESTRICT THE POSSIBILITY OF SPECIATION?

The existing ecological speciation theories, as outlined by Rundle and Nosil (2005), offer valuable insights into the dynamics that either hinder or facilitate organisms' adaptation to new hosts. According to this framework, an allele advantageous in the new host environment should experience a surge in frequency within the local population of that host. This elevation is driven by robust selection, promoting effective local adaptation. A key tenet of the theory is to safeguard the local genetic makeup from being "diluted" by incoming ancestral alleles carried by immigrants. In scenarios where mating is random and migration is frequent, maintaining the local genetic composition demands countermeasures. This can involve altering the gene mix through selective mating or by selecting specific habitats, especially when competition occurs in distinct locations. Alternatively, the influx of migrants can be curtailed to preserve the local gene pool's integrity. Multiple factors can impede the initiation of speciation and assortative mating. These include insufficient genetic diversity, the rate of genetic migration or selection during mating, and habitat preferences. Additionally, the balance between integration and isolation plays a significant role, as persistent interactions between local alleles and similarities impact their dynamics. As highlighted earlier, the success of ecological speciation in the presence of gene flow hinges on the intricate interplay of these various factors.

VI. FEATURES OF FUNGAL PATHOGENS OF PLANTS PROMOTING ECOLOGICAL SPECIATION

Numerous life history traits exhibited by fungi can promote ecological speciation by alleviating the typical constraints that impede this process. Let's delve into these features in detail and explore their implications for the potential of ecological speciation.

- 1. Abundance of Spores and Population Dynamics:** Fungi are capable of producing an extensive number of spores, reaching thousands per day, with multiple reproductive cycles generating hundreds of propagules. This implies that a single infected plant can discharge millions of spores. This prolific spore production enables population persistence and turnover, allowing the fungus to establish itself in new hosts. This phenomenon facilitates adaptation even when strong selection against hybridization prevails, and the initiation of transfer to a new host is minimal. The ample spore production also fuels rapid reproduction and genetic variation through dissemination.
- 2. In-Host and Extra-Host Mating:** Many fungi spread effectively via both mating and asexual spores. However, survival and propagation might not always accompany infection and mating, particularly in Ascomycete fungal pathogens responsible for major crop diseases. For obligate biotrophs that engage in sexual activity within the host plant, mating occurs only between individuals that can thrive on the same host. This interaction links adaptation to new hosts with local adaptation and mating patterns through pleiotropy. This "magic trait" scenario is conducive to ecological speciation, where mutations enabling adaptation to new hosts also impact mating choices. This phenomenon can limit gene flow to new hosts, even in similar environments with or without mate selection.
- 3. Integration Inside and Outside Hosts:** Whether plant pathogens integrate within or outside their hosts significantly influences gene flow between populations adapted to different hosts. For instance, consider two populations of obligate biotrophic fungal pathogens adapted to distinct host species. A biallelic haploid locus is considered, with allele A1 safeguarding against disease in host 2, while allele A2 shields against host 1 disease. Intermediate loci with host 1 B1 and B2 alleles are also involved. Barriers that can constrain gene flow include host selection, host shift, hurdles between hosts, partner selection, and postzygotic issues. In the case of obligate biotrophs that mate within a host, host adaptation itself can yield genetic impacts, as mating occurs solely among individuals able to thrive within the same host. However, if mating takes place outside the host, changing hosts might not impact gene flow at intermediate loci.

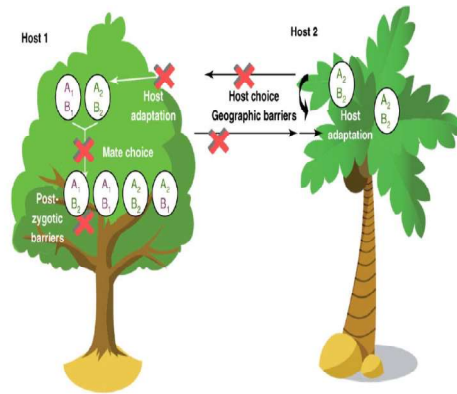


Figure 1: Lifecycle of a Pathogen Mating within its Host and the Possibility of Ecological Speciation by Host Shift

4. Role of Geographic Barriers and Mate Selection: Geographic barriers, mate selection, and postzygotic barriers can hinder gene flow at neutral B loci. Host selection and variation can affect allele frequencies, reducing allele A1 in host 2 and allele A2 in host 1 without impeding gene flow at intermediate B loci. Some basidiomycete fungi, such as rust and smut, exemplify this life cycle. Contrastingly, when a biotrophic organism requires mating within its host, host change can result in specialization and sexual isolation if mating transpires within the host environment. However, this effect diminishes if mating occurs outside the host.

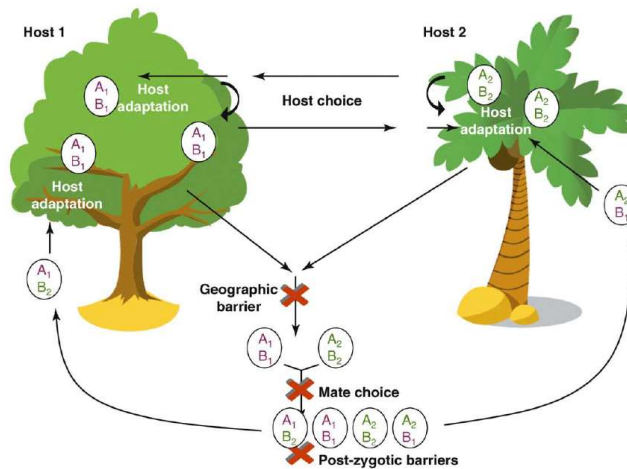


Figure 2: Lifecycle of a Pathogen Mating Outside its Host and the Possibility of Ecological Speciation by Host Shift

In sum, the unique traits of fungi, including their prolific spore production and distinct mating dynamics, provide fertile ground for ecological speciation processes. These traits can foster adaptations to new hosts and initiate the mechanisms that lead to reproductive isolation, thereby contributing to the evolution of distinct fungal lineages.

VII. SPECIES RECOGNITION IN PLANT PATHOGENS

Sex discrimination in fungi and oomycetes has historically relied on morphological and phenotypic traits. Modern techniques combine classical methods with phylogenetic analyses to discern evidence of reproductive isolation (Baum and Donoghue, 1995). This approach capitalizes on genetic disparities that hinder gene exchange, reflecting population relationships. Genetic research is often employed to augment sample size for conclusive results, revealing that fungal and oomycete species are generally twice as numerous as previously believed (Hibbett and Taylor, 2013). To incorporate molecular taxonomy, guidelines for fungal species delineation have been proposed (Dettman et al., 2003), although the relationship between these criteria for distinguishing lineages remains unclear. As such, species definition should rest on multiple independent genes with robust phylogenetic markers (Avice and Wollenberg, 1997). Various phylogenetic practices and usage of other species are examined across different contexts. Species identification poses challenges within asexual populations. Most species concepts originated for sexually reproducing organisms with shared gene pools. Thus, an adaptable framework is essential to study non-sexual or cryptic sexual stage organisms. Population genetics and evolutionary theories for asexual taxa offer insights, and multiple extensions of genetic methods have been proposed. Two prominent approaches are the K/θ method (or 4X rule) and the application of branching ratios to phylogenetic trees. The K/θ method (Birky and Barraclough, 2009) employs DNA polymorphism and coalescent theory to categorize sufficiently differentiated entities as distinct species. The average divergence between individuals is proportional to $8Ne\mu$, where N_e is population size and μ is mutation rate, with "K" representing the interval. The intraspecies polymorphism θ corresponds to roughly $2Ne\mu$. If more than 4 separate species are discernible, the 4X rule is applied. This technique recognizes species based on monophyletic shared ancestry, employing root trees to differentiate populations from bona fide species (Rosenberg, 2003). Alternatively, the determination of distinct species can be based on phylogenetic tree branch structure (Pons et al., 2006). Although more intricate than the K/θ method, this approach allows relative distinctions between branches. The null model posits that all asexual lineages remain undifferentiated, converging without evolving into ecologically distinct species. Deviations from this null hypothesis in the phylogenetic tree's structure, indicated by extended branches, serve as diagnostic indicators of divergence. Theoretical models suggest potential structural dependencies stemming from factors like changing population size or selective pressures (Kaplan et al., 1991; Rosenberg & Nordborg, 2002). While this method hasn't been extensively applied to plant diseases, it can be coupled with the K/θ method to identify species and estimate speciation rates. Together, these techniques advance our understanding of fungal and oomycete diversity, shedding light on their evolutionary histories and reproductive boundaries.

- 1. Speciation and the Emergence of New Diseases:** Comprehending the origins of emerging diseases is crucial for effective management and prevention strategies (Ahmed et al., 2012; Stukenbrock and McDonald, 2008). Genetic investigations into fungal and oomycete evolution offer insights into the rise of novel diseases, often indicating instances where pathogens adapted or evolved to trigger new infections. These events unfold through one of three primary processes.
- 2. Spatial Colonization without Speciation:** In simpler cases, the emergence of new diseases doesn't entail the evolution of distinct species. This scenario occurs when a

pathogen enters a new geographic area and encounters host species it traditionally infects in its ancestral habitat. A prime example is *Mycosphaerella fijiensis*, which has caused a recent global epidemic in banana plantations. Molecular analyses suggest that much of the disease spread is attributed to population bottlenecks (where populations significantly decrease), with disease dissemination possibly facilitated by the movement of plant ascospore material (Halkett et al., 2017). A similar pattern was observed in the case of *Phytophthora* causing sudden oak death. These pathogens harbor various genetic variants that likely evolved long before modern agriculture (Goss et al., 2009).

- 3. Adaptation to New Hosts:** Another process involves pathogen colonization of a new environment, followed by the acquisition of the ability to infect novel hosts. This adaptation occurs through host change or expansion, enabling the pathogen to thrive in a host different from its progenitor. Speciation often accompanies the emergence of new pathogens, driven by new mutations leading to divergence from the parent species. For instance, the pathogen *Heterodera schachtii*, responsible for scalding disease, exhibits three cryptic strains evolving through ecological diversification and host specificity in barley, rye, and wheatgrass (Zaffarano et al., 2008). Genetic analyses have revealed host-specific pathogens like *Colletotrichum kahawae*, which targets green coffee (Silva et al., 2017). Recent outbreaks of such diseases have been linked to changes in host preference, highlighting agriculture's role in disease dynamics.
- 4. Hybridization and Novel Mechanisms:** The third possibility involves a combination of the previous two scenarios. In this case, hybridization generates new mechanisms not present in the parent organisms. This leads to the emergence of a distinct form of disease, often referred to as transboundary segregation, which enables infection in a new host. Hybrids and the mixing of similar organisms following exposure can facilitate disease transmission across species boundaries (Gladieux et al., 2011).

To gain further insights into the boundaries of phytopathogenic species, demographic analyses of gene transfer within a well-defined spatial context offer valuable information. These investigations shed light on the intricate interplay of factors driving the emergence and transmission of plant diseases.

VIII. SOME IMPLICATIONS OF LINKING EMERGING DISEASES AND ECOLOGICAL SPECIATION

It's widely acknowledged that diseases caused by fungal phytopathogens primarily result from host adaptation, and the diverse nature of these pathogens offers valuable insights into species evolution and fungal biodiversity dynamics. This ecological understanding contributes to our comprehension of disease development and change, as well as the formulation of effective strategies.

- 1. Implications for Disease Management and Classification:** Recognizing the significance of host adaptation for speciation has important ramifications. If host adaptation alone sufficed for speciation, the criterion of sterility (commonly used for species definition) might not be essential. In cases where the only reproductive challenge is host shift, sterility could persist even after gene flow between phytopathogenic populations stops. Disregarding the positive role of host adaptation could lead to treating

distinct diseases as a single entity, potentially influencing management approaches like specific fungicides. Precise species identification forms the basis for crafting exceptions and appropriate strategies, aligning management with the unique characteristics of each taxon. Rapid host switching also has implications for exceptions to host switching, necessitating swift decisions on species classification.

2. **Linking Disease Outbreaks to Ecological Speciation:** Connecting disease outbreaks with ecological speciation is crucial to assessing whether new diseases stem from dispersal, host expansion, or host shift. These different scenarios impact disease control methods, such as fungicide use against specific hosts. Disease diversity and adaptation differ between diseases that adapt to a single host versus those targeting multiple hosts or engaging in host-versus-host interactions (Anwar *et al.*, 2008).
3. **Considerations for Theoretical Models and Disease Threats:** The sufficiency of host change for generating new pathogens can lead to rapid disease outbreaks, an aspect that theoretical models aimed at predicting disease outcomes should account for. Evolutionary patterns of fungal diseases, including virulence, should reflect the unique nature of disease life cycles. Modeling the interactions between organisms and their hosts, as exemplified by the Quantinemo software package, should accommodate distinctions between selection and mating.
4. **Influence on Isolation Policies and Control Measures:** The specific life cycle of fungal plant diseases should guide assessments of disease threats. Diseases that coexist harmoniously within one host might become more harmful when introduced to new hosts. Such insights should inform isolation policies, production control, and cultivation practices.

Overall, understanding the ecological basis of disease emergence and the intricate relationships between fungal phytopathogens and their hosts enhances our ability to effectively manage and prevent plant diseases. It also guides research and policymaking in the realm of agricultural sustainability and biosecurity.

IX. CONCLUSION

In conclusion, recent years have witnessed significant progress in the study of fungal speciation, with robust biological models being introduced that have broader implications for speciation research. Fungi exhibit distinct and intriguing speciation patterns, yet numerous unresolved inquiries remain ripe for exploration. Novel techniques for investigating historical genetic variations are now available, offering insights into where fungal speciation occurs, ranging from specialization within homologs to adaptation to new hosts. Evolutionary biology serves as a solid foundation for understanding the origins of organisms (Xhaard *et al.*, 2011).

Emerging as a promising field, the study of evolutionary processes in plant pathogens presents the potential to unveil fresh models and perspectives on speciation and adaptation. At a pragmatic level, the integration of diverse data sources will enable the identification of pathogenic genes in phylogenetic contexts, facilitating comparative analyses to decipher the population dynamics of plant diseases. A fundamental aim of phytopathology is to predict the

emergence of new diseases, an objective that can be pursued through an evolutionary lens. By combining classical methodologies with high-resolution genomic investigations, the intricate population and genetic attributes underlying speciation events in oomycete and fungal plant diseases can be unveiled. These advanced techniques complement traditional methods and problem-solving strategies. Delving into the evolution and dynamics of plant diseases provides valuable insights into their historical impact on agriculture. Recent research on various diseases holds the potential to shed light on pivotal questions in evolutionary theory. What extent of gene flow is required to counteract diversity through selection? How does hybridization contribute to the generation of new organisms? Do hybrid progenies exhibit novel traits or are they consistently inferior to their parents? Does hybridization and amalgamation lead to species convergence? These inquiries not only form the crux of evolutionary biology exploration but also bear immediate relevance to contemporary disease management strategies, offering fundamental insights into the fundamental origins and processes driving the emergence of novel diseases.

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