

11 **Convergent Adaptation and Specialization of Eukaryotic Pathogens across Agricultural Systems**

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Domestication of crops provides an opportunity for pathogens to exploit novel, abundant hosts. Pathogens specializing on human crops have repeatedly emerged over the history of human agriculture. Similarly, pathogens have tracked domestication of the fungal crops of ants (Caldera et al. 2009). Like pathogens in nondomesticated systems, agricultural pathogens often face selection pressures to overcome host defenses, and such adaptation may lead to increased specialization (Flor 1956; Burdon 1987; Thompson and Burdon 1992). Specialization may lock pathogens into narrow host ranges, such that as host crops diverge from one another, either through intentional or unintentional selection by their domesticators, pathogens also diverge, potentially leading to patterns of co-divergence between the pathogens and their hosts. Alternatively, despite specialization, pathogens may make occasional host jumps, switching to hosts distantly related to the original host, which can lead to the emergence of novel disease.

Here, I highlight four key issues in the study of crop pathogen evolution and specialization and the approaches used to address those questions, focusing on fungal and oomycete pathogens in human and ant agriculture. These include (1) using experimental and molecular approaches to compare pathogens in domesticated and nondomesticated systems in order to determine the origins of crop pathogens; (2) elucidating the relationships between pathogen strains that utilize different crops to gain insights into the degree and evolution of pathogen specialization; (3) leveraging genomics and genetics to elucidate the mechanisms underlying pathogen specialization; and (4) studying how, like their crop hosts, pathogens evolve in response to agricultural practices. In many cases, we have more advanced understanding of human crop pathogens, but the study of ant crop pathogens provides a unique opportunity to study crop pathogen evolution over a much longer time scale.

The Diversity of Eukaryotic Pathogens Attacking Human and Ant Crops

Over the last 12,000 years, humans have domesticated a broad array of plant and fungal crops. All of these crops are parasitized by pathogens. The impact of pathogens on crop yield and crop quality has profoundly shaped human agriculture. Over the history of agriculture, humans have abandoned some crop varieties because of high pathogen burdens

(Heslop-Harrison and Schwarzacher 2007). Humans also have minimized disease through selection for crop resistance and through use of management strategies and chemical fungicides to minimize pathogen spread and pathogen damage.

The pathogens of human crops are as diverse as the crops themselves. In many agricultural systems, fungal and oomycete pathogens cause the most disease burden. Some of these pathogen species are described as being specialized (e.g., *Blumeria* spp., *Puccinia* spp., *Ustilago* spp.; table 11.1) (León-Ramírez et al. 2004; Dracatos et al. 2018), with each species attacking only one or a few host species, or, at a finer scale, with strains within a species being able to attack only certain genotypes of a given host species. Other pathogen species are considered to have broad host ranges (e.g., *Botrytis cinerea*, *Fusarium oxysporum*, *Phakopsora pachyrhizi*, *Rhizoctonia solani*; table 11.1) (Goellner et al. 2010; Dean et al. 2012; Hane et al. 2014), though within these species there may be fine-scale specificity due to genotypic interactions and local adaptation to both abiotic and biotic factors as well. Pathogens also differ in their level of virulence and economic impact.

Humans are not the only farmers. Agriculture, defined here as large-scale dispersal, seeding, and management of food propagules that are sustainably harvested, is a feature of other animal systems as well (introduction, this volume). Nonhuman agriculture is dominated by domestication of microbial crops (though see chapter 9, this volume). Slime molds cultivate bacteria (Brock et al. 2011). Snails cultivate fungi (Silliman and Newell 2003), as do ants, termites, and beetles (Mueller et al. 2005). While crop pathogens have not been identified in many of these systems, identification of a specialized fungal pathogen in the fungus-farming ant system has made the system a model for studying host-pathogen evolution. The primary pathogens in the ant system are fungi in the genus *Escovopsis*.

Fungus-growing ants have evolved for 50 million years into more than 245 species in over 19 genera of obligate farmers that propagate their cultivated fungi primarily vertically between the nests of mothers and daughters (Schultz and Brady 2008). Like human populations specialized at growing particular crops, most species of ants grow a narrow range of fungal cultivars (Mueller et al. 2018). *Escovopsis* spp. parasites attack and consume the fungal cultivars, which can lead to rapid colony decline (Reynolds and Currie 2004; Currie 2001). Different *Escovopsis* spp. attack different fungal crops (Currie et al. 2003; Gerardo et al. 2004; Gerardo, Mueller, and Currie 2006; Pagnocca, Masiulionis, and Rodrigues 2012; Custodio and Rodrigues 2019). To manage *Escovopsis* infections, ants actively eliminate infected portions of garden (Currie and Stuart 2001) and use antibiotic-producing bacteria that suppress fungal infection (Currie et al. 1999; Poulsen et al. 2009).

Human and ant agricultural systems exhibit many similarities as they relate to disease transmission and management (figure 11.1). For example, in both human and ant agriculture, crops are typically grown as monocultures of single species (Mueller et al. 2010; McDonald and Stukenbrock 2016), which leads to high host density relative to density of nondomesticated hosts (chapter 4, this volume). This may facilitate transmission within fields (human agriculture) and within colonies (ant agriculture). At the same time, these field and colony patches may be spatially separated from one another, which could lead to pathogen extinction at local scales or pathogen adaptation to local hosts and conditions (i.e., local adaptation) (Croll and McDonald 2017). Furthermore, pathogens of both human and ant agriculture must contend with an array of defense strategies, including utilization of behavioral and chemical defenses. Crop rotation, for example, is a behavior employed

Table 11.1
Key fungal and oomycete pathogens of human crops

Pathogen	Host crop(s)	Disease	Notes on specialization
<i>Blumeria graminis</i> ^F	cereal crops and other grasses	powdery mildew	Genetic analyses indicate that strains cluster according to host range, suggesting specialization of groups within the species (Wyand and Brown 2003).
<i>Botrytis cinerea</i> ^F	broad host range, including grapes	gray mold, noble rot	While there is some evidence of adaptation to alternative agricultural host plants, strains have very broad host ranges and show little evidence of specificity (Bardin et al. 2018).
<i>Colletotrichum</i> spp. ^F	broad host range, including bananas, cassava, and many stored fruits	anthracnose spots and blights, post harvest blights	The phenomenon of cultivar specificity was first recognized in <i>C. lindemuthianum</i> .
<i>Fusarium graminearum</i> ^F	cereals, maize	fusarium head blight	Infection across host species indicates little evidence for specificity (Kuhnem et al. 2015).
<i>Fusarium oxysporum</i> ^F	broad host range, including bananas	fusarium wilt	While the species is considered to have a broad host range, individual isolates are highly specialized.
<i>Melampsora lini</i> ^F	flax, linseed	flax rust	<i>M. lini</i> serves as a model for studying gene-for-gene specificity in pathogen-plant relationships (Flor 1956).
<i>Mycosphaerella graminicola</i> (syn. <i>Zymoseptoria tritici</i>) ^F	wheat	<i>Septoria tritici</i> blotch (STB)	While <i>M. graminicola</i> is specific to wheat, other <i>Mycosphaerella</i> spp. infect other grasses. Comparative genomics and genetic manipulations have elucidated some aspects of host specialization (Poppe et al. 2015; Stukenbrock et al. 2011).
<i>Phakopsora pachyrhizi</i> ^F	broad host range, including soybean and many legumes	Asian soybean rust	It is not clear whether this species' broad host range is due to unusual plasticity for a rust fungus or whether there are underlying intraspecific populations that differ in virulence and host specificity (Ono, Buriticá, and Hennen 1992).
<i>Phytophthora infestans</i> ^O	potato, tomato	late blight, tomato blight	<i>P. infestans</i> is closely related to other species with different host ranges.
<i>Puccinia</i> spp. ^F	cereals	rust	Strains are host specific, though they can infect alternative hosts at certain stages.
<i>Pyricularia graminis-tritici</i> ^F	wheat	wheat blast	<i>P. graminis-tritici</i> is part of a species complex that can cause disease on a variety of grasses. There is debate as to whether this should or should not be split from <i>P. oryzae</i> (Gladieux et al. 2018; Valent et al. 2019).

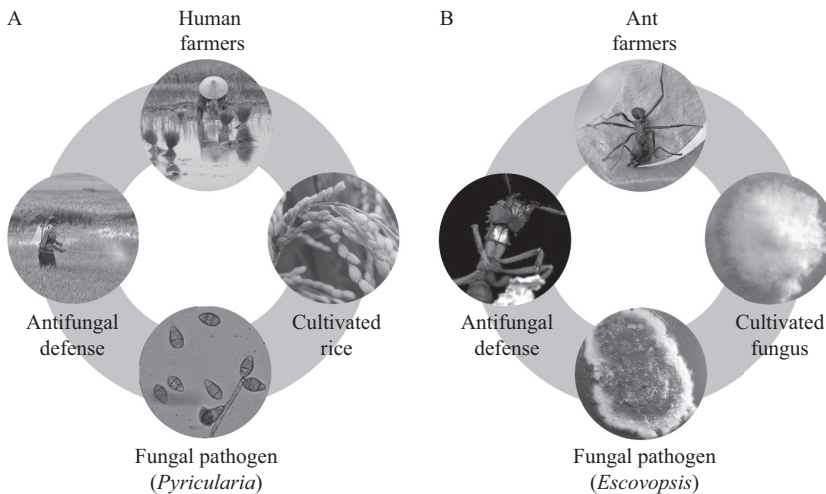
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Pathogen	Host crop(s)	Disease	Notes on specialization
<i>Pyricularia oryzae</i> (syn. <i>Magnaporthe oryzae</i>) ^F	rice	rice blast	<i>P. oryzae</i> is part of a species complex that can cause disease on a variety of grasses, though the name <i>P. oryzae</i> is sometimes used only for those that infect rice. Several genes have been identified that may underlie host specificity (Yoshida et al. 2016).
<i>Rhizoctonia solani</i> ^F	broad host range, including cereals, beans, and brassica	damping off, seed rot, root rot, black scurf and other diseases	Some groups of strains may be more specific than others (Keijzer et al. 1997).
<i>Ustilago maydis</i> ^F	corn	corn smut	While host species-specific in nature, <i>U. maydis</i> can infect a broad range of hosts under lab conditions (León-Ramírez et al. 2004).

Notes: List of eukaryotic pathogens based on previous surveys of plant mycologists to identify fungal pathogens of plants that are of economic concern or that serve as models for studying fungal disease (Dean et al. 2012). Additional fungal and oomycete pathogens of human crops mentioned in the text have been added.

^Ffungal pathogen, ^Ooomycete pathogen.

**Figure 11.1**

Parallels between farmer-crop-pathogen interactions. (A) The role of pathogens in shaping human agriculture is exemplified by infection of rice by the fungal pathogen *Pyricularia oryzae* (syn. *Magnaporthe oryzae*). Human farmers (top) actively cultivate rice (right) in large monoculture fields. *P. oryzae* infects rice, causing rice blast. To combat the disease, humans use an array of defense strategies, including chemical fungicides (left). (B) Leaf-cutting ants (top) cut fresh vegetation to feed to their cultivated fungus (right), which is grown in monoculture within ant colonies. The cultivated pathogen is attacked by fungal pathogens in the genus *Escovopsis* (bottom). To combat infection, the ants deploy an array of defenses, including the use of antimicrobials produced by bacteria that grows on the ants' cuticles (white patch under the ant's head, left). Ant photographs: Alex Wild.

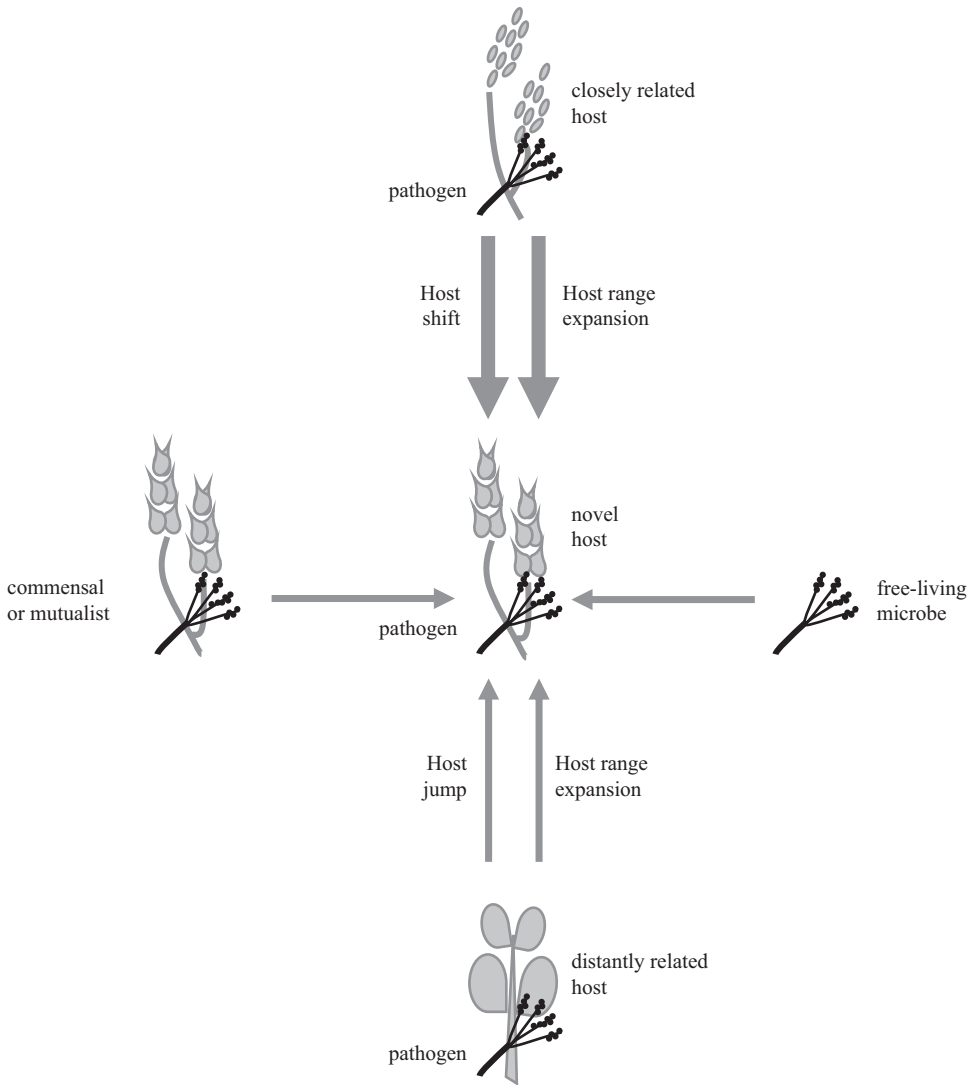
by humans to minimize pathogen build-up in fields. While ants do not switch crops readily (Mueller, Poulin, and Adams 2004), they can invest heavily in weeding their gardens to remove pathogens (Currie and Stuart 2001). Humans utilize a suite of defensive chemicals (e.g., fungicides) to combat pathogens at great expense, and ants utilize bacteria that produce antifungals to inhibit their gardens' pathogens (Kelly and Ward 2018). Humans also both consciously and unconsciously select for crops with higher resistance. While there is no direct evidence that ants do the same, there has been ample time over the millions of years of ant-cultivar-*Escovopsis* association for the ants to at least occasionally propagate more resistant crop strains. These parallels could lead to convergent processes of pathogen evolution in these systems.

Studying the Origins of Crop Pathogens

There are several potential mechanisms by which pathogens may begin to utilize crops as hosts. These include host range expansion (i.e., beginning to utilize a new host while retaining the ability to utilize current hosts), host shifts (i.e., switching to utilize a new host closely related to the current host), host jumps (i.e., switching to utilize a new host distantly related to the current host), and adaptation to a pathogenic lifestyle from a free-living, commensal, or mutualistic form (figure 11.2). Host range expansion, host shifts, and host jumps require contacting novel hosts, which can be facilitated by migration. In human agriculture, for example, migration and colonization have played an important role in the establishment of novel pathogens (Goodwin, Cohen, and Fry 2006). Whether a pathogen begins to associate with a crop due to range expansion, host shift, or host jump, the ancestral host could be either a nondomesticated or a domesticated species.

Determination of the origins of a pathogen relies on comparative analyses across pathogen species or strains isolated from alternative hosts. In some cases, patterns will be clear, highlighting relationships between pathogens that suggest the origins of novel infections. Dating methods can provide insight into when a pathogen emerged in an agricultural system. Phylogenetic analyses of *Pyricularia* spp. (syn. *Magnaporthe* spp.) strains isolated from a variety of grass species, for example, indicate that *P. oryzae*, a virulent pathogen of rice, originated from a host jump from millet to rice. It then made several host shifts from rice to grassy weeds associated with farming (Couch et al. 2005). Similarly, phylogenetic relationships of isolates of *Phytophthora infestans*, the causal agent of the Irish Potato Famine, are consistent with a hypothesis that the virulent pathogen spread from Mexico, where diverse potato varieties are grown. Of note is that there is substantially more genetic variation in the Mexican *Phytophthora* population, which suggests that the pathogen went through a series of bottlenecks as it spread globally (Goodwin, Cohen, and Fry 2006).

Experimental infections can also suggest something about pathogen origins. *Pyricularia graminis-tritici* is an emerging pathogen of global concern. In Brazil and surrounding countries in South America, it has consistently caused wheat losses of 40–100% since first being reported in 1985 (McDonald and Stukenbrock 2016; Ceresini et al. 2018). It has also been reported in Bangladesh, where it has also caused devastating crop losses (Islam et al. 2016). While it was suspected that the pathogen originated by a host shift of *Pyricularia* found on rice to wheat, experiments demonstrated that *Pyricularia graminis-tritici* strains

**Figure 11.2**

Origins of crop pathogens. Novel agricultural pathogens can arise from a number of sources. Common routes (top) include pathogens that evolve to use a novel host that is closely related to the original host. This can occur through host shifts, when populations or variants of the pathogen evolve to use the novel host and lose the ability to infect the original host, or host range expansion, when pathogens evolve to become more generalist, being able to infect both the original and novel host. Less common are host jumps (bottom), where pathogens evolve to infect novel hosts distantly related to the original host, or host range expansion, where pathogen host range evolves to include distantly related hosts. While not commonly observed, there is the potential for free-living (non-host associated) (right) and commensal and mutualistic microbes (left) to evolve into host-associated pathogens.

are not virulent on rice; this suggests that they instead originated from strains infecting a different grass host (Urashima, Igarashi, and Kato 1993; Castroagudín et al. 2016).

For *Escovopsis* spp., the only known pathogens of ant-cultivated fungi, the first phylogenetic analyses based on samples of *Escovopsis* and cultivars associated with a subset of ant species demonstrated phylogenetic congruence between the ants, their cultivars, and *Escovopsis* (Currie et al. 2003). This is consistent with a process of strict specialization and host fidelity such that pathogen species, once they emerge, rarely switch to new hosts through host jumps. Deeper sampling, however, indicates that the evolutionary history of the pathogen has included at least occasional jumps to distantly related hosts (Gerardo, Mueller, and Currie 2006; Meirelles et al. 2015).

For many human crop pathogens, such as *P. oryzae* mentioned above, researchers have identified closely related pathogen strains living on free-living hosts; this finding has facilitated determination of how and when the pathogens of domesticated crops diverged from free-living associates. No putative free-living relatives of *Escovopsis* have been identified. Assuming that the ancestor was a pathogen itself, further sampling of fungal pathogens of nondomesticated, free-living fungi in the Neotropics could potentially identify such a relative. Limited dating does suggest that the origin of the *Escovopsis* genus may be ancient and coincident with the evolution of ant agriculture (de Man et al. 2016). Such dating methods should be extended to comprehensively investigate the origins of clades within the *Escovopsis* genus.

Experimental Approaches, Phylogenetics, and Population Genetics Elucidate Patterns of Specialization

A defining feature of many host-pathogen systems is arms race coevolution, where there is strong selection on hosts to resist pathogens and strong selection on pathogens to overcome resistance (Haldane 1949). These processes can lead to the establishment and maintenance of specialization by pathogens because selection for the ability to infect and overcome resistance in some hosts leads to loss of the ability to effectively utilize other hosts (Flor 1956; Burdon 1987; Thompson and Burdon 1992), though this depends on the genetic basis of host resistance and pathogen virulence (Parker 1994).

In some respects, the degree to which a pathogen species is considered specialized is dictated by how we define a species. If ecological isolation based on utilization of alternative hosts precludes genetic exchange between two or more pathogen populations, then, by the biological species concept, researchers may define these two populations as separate species (Restrepo et al. 2014). In tandem or alternatively, phylogenetic species concepts may be utilized to name species based on the formation of monophyletic groups. Regardless of how a species is defined, specialization can be investigated by comparing the ability of different species or strains within species to infect a set of hosts. Experimental investigation can be coupled with phylogenetic and population genetic investigations to elucidate the relationships between strains found on different hosts in nature.

A common approach to study pathogen specialization is to screen the ability of strains isolated from different environments to utilize different hosts. These experiments can provide insight into the degree of host specialization (how many hosts a pathogen can use)

and the breadth of host range (how closely related useable hosts are to one another). Cross inoculations of potato and tomato with strains of *P. infestans* isolated from both crops, for example, indicates that potato strains are specialized on potato, having very low fitness when put on tomato. Tomato strains are more generalist, though they do perform better on tomato than potato (Kröner et al. 2017) (figure 11.3A). Similar cross inoculations have been conducted utilizing *Escovopsis* isolated from colonies of different ant species that grow distinct fungal crops. Like *P. infestans*, these *Escovopsis* strains are more likely to successfully infect their typical than their atypical host (Gerardo et al. 2004, 2006; Birnbaum and Gerardo 2016) (figure 11.3B). Also like *P. infestans*, some *Escovopsis* strains appear to be more generalist than others (Birnbaum and Gerardo 2016).

Phylogenetic and population genetic analyses of many strains from different hosts can also provide insights into the degree of host specialization. Experimental results suggesting that *P. graminis-tritici* is specialized on wheat (Urashima, Igarashi, and Kato 1993; Castroagudín et al. 2016), for example, are consistent with population genetic analyses that demonstrated that rice- and wheat-infecting strains form distinct genetic clusters with little evidence for gene flow between them (Chiapello et al. 2015), though with evidence of some gene flow between strains infecting wheat and other hosts (e.g., oats) (Gladieux et al. 2018). Furthermore, phylogenetic analyses corroborated the host specificity of lineages and revealed that wheat-infecting *P. graminis-tritici* are more closely related to strains found in association with oats than they are to strains found in association with rice (Castroagudín et al. 2016; Yoshida et al. 2016). Thus, these analyses together elucidated both the origins and specialization of this fungal pathogen.

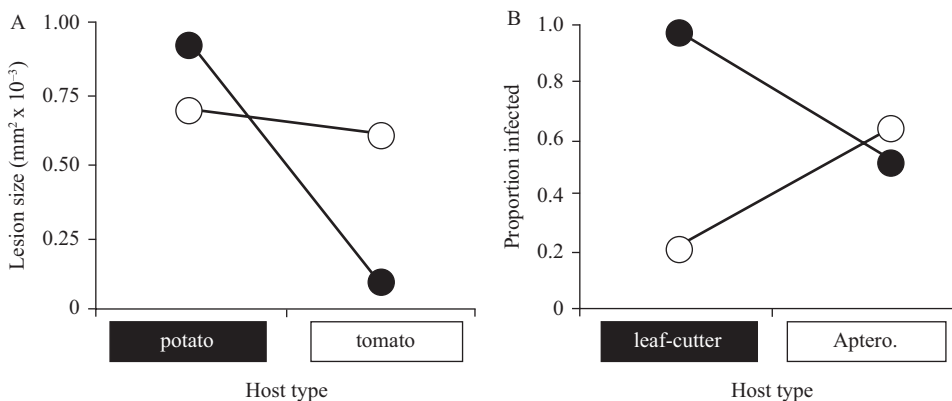


Figure 11.3

Parallel investigation of pathogen host range. The host ranges of pathogen strains are often investigated by doing cross-inoculations of alternative hosts with pathogens isolated from those hosts. Specificity is exemplified by pathogens being able to better infect their native host than an alternative host. This is exemplified by (A) cross inoculations of potato and tomato plants with strains of *Phytophthora infestans* (black indicates strains from potato, and white indicates strains from tomato; figure adapted from Kröner et al. 2017)); and (B) cross inoculations of cultivated fungi from leaf-cutter and *Apterostigma* ant colonies with strains of *Escovopsis* spp. (black indicates strains from leaf-cutter colonies [*Atta* and *Acromyrmex* spp. combined], and white indicates strains from *Apterostigma* colonies); figure adapted from Birnbaum and Gerardo (2016). Note that, in the former case (A), infection success is measured by the virulence of the pathogen, as measured by the size of lesions created by the infection, while in the latter case (B) infection success is measured by establishment of the pathogen on the hosts, as measured by the proportion of hosts that are infected.

Phylogenetic investigations of *Escovopsis* have demonstrated that, at the broad scale, *Escovopsis* spp. are specialized on particular cultivar hosts (Currie et al. 2003; Gerardo, Mueller, and Currie 2006). At finer scales, population genetic analyses of *Escovopsis* strains isolated from different colonies of the same ant species that are growing closely related cultivars often indicate that genetic distances are not correlated with differences in host utilization (Gerardo and Caldera 2007; Taerum et al. 2007). This contradicts both genetic and experimental studies with other *Escovopsis* strains that highlight that closely related strains of the same *Escovopsis* spp. may differ in which cultivar strains they can infect, which suggests that *Escovopsis*-cultivar dynamics can exhibit genotype-genotype specificity (Birnbaum and Gerardo 2016; Kellner et al. 2018; Custodio and Rodrigues 2019). These differences suggest that some *Escovopsis* spp. are more generalist than others.

The Use of Genetics and Genomics to Reveal Mechanisms of Host Utilization and Specialization

Several fungal and oomycete pathogens of human crops have been developed as tractable genetic models to study the evolutionary dynamics of interactions between species. For example, the model for gene-for-gene matching between pathogen genes underlying virulence (known as “avirulence” genes) and host genes underlying resistance was first described for *Melampsora lini*, a fungal pathogen of flax and linseed (Flor 1956). While not of huge economic concern, the genetic tractability of this plant-pathogen system is a model for studying plant resistance, plant immunity, and mechanisms of pathogen virulence (Chisholm et al. 2006; Dean et al. 2012). Other fungal pathogens of agricultural crops have demonstrated how both multigenic, quantitative traits and ecological conditions can shape the outcomes of host-pathogen interactions (Croll and McDonald 2017).

While genetic technologies for some crop pathogens have been available for decades, the utilization of genomics to investigate eukaryotic pathogens has provided novel insights into the genetic underpinnings of host utilization and host specialization in many systems without tools for genetic manipulation. Crop pathogen genome sequencing efforts have identified genes that may underlie host utilization and virulence, including genes involved in secondary metabolism, carbohydrate utilization, and manipulation of host metabolism (Dean et al. 2005; Kämper et al. 2006; Chiapello et al. 2015). Genomes of crop pathogens have also revealed that eukaryotic crop pathogens differ markedly in their genomic structure and organization. For example, while some fungal pathogens have streamlined genomes (de Man et al. 2016; Benevenuto et al. 2018), others are packed with repetitive elements and have large genomes (Raffaele and Kamoun 2012), suggesting that these organisms adapt to hosts under fundamentally different genomic constraints.

Comparative genomic projects have moved beyond the annotation of single genomes to investigate differences between strains or closely related species that utilize different hosts. For example, comparison of the genomes of eight *Pyricularia oryzae* (syn. *Magnaporthe oryzae*) strains that differ in host specificity revealed that the gene content and genomic features of these genomes are highly similar. One notable signature of host specialization, however, is that strains adapted to rice share a specific set of gene families that are not found in the strains attacking other hosts (and vice versa). The rice-specific

gene families include known avirulence genes and some genes involved in secondary metabolism (Chiapello et al. 2015). Beyond identifying differences in the presence and absence of genes, comparative genomic approaches can also assess signatures of selection across genomes, potentially revealing those regions that may be under selection because of their role in host-pathogen interactions. For example, many human crop pathogens exhibit diversifying selection at loci underlying virulence (van de Wouw et al. 2010; Kelly and Ward 2018). Other studies assessing patterns of positive selection across pathogen genomes adapted to different hosts have revealed complex patterns of selection across many loci; this finding suggests that adaptation to hosts may involve multigenic selection on genes underlying interaction with both abiotic and biotic stressors (Benevenuto et al. 2018; Mohd-Assaad, McDonald, and Croll 2018). Results from these genome-wide studies suggest that the prevailing view of pathogen evolution being defined by a few loci underlying pathogen-host gene-for-gene interactions may be missing key elements of pathogen adaptation to the environment.

Molecular investigations of the mechanisms underlying *Escovopsis* specialization in the ant agricultural system are in their infancy. Sequencing and annotation of the first *Escovopsis* genome provided some insights into the basis of *Escovopsis*'s host utilization (de Man et al. 2016). As with human crop pathogens, *Escovopsis* genomes encode for the capacity to produce a rich array of secondary metabolites (de Man et al. 2016; Heine et al. 2018) and to utilize carbohydrates abundant in their fungal crop hosts. Of note is that the genome annotation revealed that *Escovopsis* cannot produce key enzymes necessary for utilizing plant material that can be abundant in ant gardens—a finding that highlights that it is indeed a specialized pathogen of the ants' fungal crop (de Man et al. 2016). Comparative genomics across *Escovopsis* spp. associated with different hosts may reveal how these features change with host range. As with human crop pathogens, development of tools for genetic manipulation could greatly facilitate study of the evolution of *Escovopsis* specialization.

Consideration of How Agricultural Practices Shape Pathogen Evolution

Due to their large population sizes, short generation times, and ability to disperse, eukaryotic pathogens have amazing potential to adapt to abiotic and biotic selection pressures, including agricultural practices. Because of its applied importance and experimental tractability, one of the most common phenotypes studied in this regard is the evolution of resistance to fungicides. Resistance in fungal pathogens appears to often arise via *de novo* mutations in the target sites of the fungicides (Hawkins et al. 2019). The mutations can then spread rapidly, shaping pathogen population structure in agricultural settings (Kozhar et al. 2020).

The fungus-growing ant system provides a particularly interesting case study in terms of how pathogens adapt to host defenses. Unlike humans, who typically use chemical fungicides in agriculture, ants use fungicides produced by bacteria (Currie et al. 1999). Evolution of fungicide resistance in the pathogens could select for the ants to switch to novel bacterial partners that produce alternative fungicides or could select for the bacteria to modify the fungicides that they produce. While *Escovopsis* spp. and strains within species vary in terms of their susceptibility to these bacteria-derived fungicides (Poulsen et al. 2009), nothing is known about the mechanisms of resistance. Elucidation of these

mechanisms could open up avenues to explore how fungicide resistance evolves in this ancient agricultural system and whether the pathogens and fungicide-producing bacteria evolve in response to one another in an arms-race-like fashion.

Another feature of agriculture that can shape pathogen evolution is the spatial structure of the agricultural landscape (Papaix et al. 2015). Large, uniform monocultures, for example, may facilitate the evolution of pathogen specialization (Débarre and Gandon 2010), whereas landscape heterogeneity, providing potential reservoirs of noncrop host species, could hinder the evolution of specialization. Crop harvest and rotation practices, both of which influence host density and availability, may also influence pathogen evolution, particularly evolution of traits that influence transmission and virulence (van den Berg et al. 2011). A proxy for spatial structure in ant agriculture is colony density and proximity to colonies of the same or other species. These community features have not yet been considered in terms of their impacts on cultivar-*Escovopsis* disease dynamics over ecological time or evolution over longer time scales.

Conclusions and Implications

Pathogens place strong evolutionary pressures on their hosts and have shaped domestication processes. Because pathogens can be spread with their hosts and can diversify along with their hosts, studying pathogen diversification may inform our understanding of ancient domestication processes. Understanding the origins and adaptive processes of current pathogens in agricultural systems can also have important applied implications. The degree of specialization of crop pathogens and the mechanisms underlying this specialization can provide insight into the likelihood of disease spread and can therefore inform management strategies. Furthermore, if studies across agricultural pathogen systems indicate similar origins for many pathogens, as they do with zoonotic diseases, then the routes of transmission that facilitate these origins may be more carefully controlled to minimize the emergence of novel diseases. Beyond these applied reasons for studying agricultural pathogens, these systems can serve as models for studying evolutionary processes. These experimentally tractable systems, for example, allow researchers to explore the proximate and ultimate mechanisms underlying coevolution and co-speciation.

Acknowledgments

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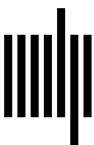
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