Evolution, Diversity, and Taxonomy of the Peronosporaceae, with Focus on the Genus *Peronospora*

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ABSTRACT

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Downy mildews are a notorious group of oomycete plant pathogens, causing high economic losses in various crops and ornamentals. The most species-rich genus of oomycetes is the genus *Peronospora*. This review provides a wide overview of these pathogens, ranging from macro- and micro-evolutionary patterns, their biodiversity and ecology to short overviews for the currently economically most important pathogens and potential emerging diseases. In this overview, the taxonomy of economically relevant species is also discussed, as the application of the correct names and species concepts is a prerequisite for effective quarantine regulations and phytosanitary measures.

Additional keywords: evolutionary biology, plant pathology.

EVOLUTION OF OOMYCETES AND OBLIGATE BIOTROPHY

Oomycetes are a group of straminipilous organisms and evolved fungal-like characters in parallel with the true fungi (Beakes et al. 2014). The roots of oomycetes are not fully understood, but the Oomycota seem to stem from biflagellate, free-ranging predatory protists (Beakes et al. 2012), such as *Pirsonia* and *Developayella*. The basal oomycete lineages are predominantly marine and are holocarpic pathogens of nematodes, algae, crustaceans, and mollusks (Beakes et al. 2012; Sekimoto et al. 2008). The transition to a terrestrial or limnic lifestyle has been made at least four times, once in the basal oomycete genus *Haptoglossa*, once in the basal oomycete genus *Olpidiopsis*, and twice in the crown oomycete groups, the Saprolegniomycetes and the Peronosporomycetes. Both crown groups contain both eucarpic and holocarpic species, and it seems that after the novelty of hyphal growth had evolved, at least two

reversions to holocarpy occurred, once in the lagenidiaceous fungi (e.g., *Lagena*, “*Lagenidium*” [Blackwell 2011]) and once in the Saprolegniomycetes (Thines et al. 2015).

A hallmark of the oomycetes is the formation of sexual resting spores, the so-called oospores. These seem to be present in the vast majority of the crown oomycetes, but there are only few reports from oomycetes that are more basal, such as *Olpidiopsis* species (Sekimoto et al. 2008). It is unclear at which time during oomycete evolution oospores came into existence, and it seems possible that oospore formation has been lost several times during evolution (Thines et al. 2015), with sexual reproduction, e.g., by the fusion of gametes, as suggested for *Lagenisma coscinodisci* (Schnepf et al. 1978), but also for the basal oomycete genus *Eurychasma*. The diversity of the basal oomycete clades is vastly unexplored and more than 95% of the about 2000 known oomycete species have been described from the crown groups, the peronosporalean (Thines 2014) and saprolegnialean oomycetes (Sparrow 1976). In both of these major groups, plant pathogenicity has evolved. In the Saprolegniomycetes, some plant pathogens are found in the Verrucalvaceae, e.g., *Aphanomyces euteiches*, *Verrucalvus flavofaciens*, and *Pachymetra chaunorhiza* (Dick et al. 1984, 1989; Gaulin et al. 2007). However, these few saprolegnialean plant pathogens are opposed by about 1000 plant pathogenic species in the Peronosporomycetes (Thines 2014), the vast majority of which

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are found in the orders Albuginales and Peronosporales. In both of these orders, obligate biotrophy has evolved independently, a lifestyle where the pathogens are fully dependent on living plant host cells for their nutrition. While the Albuginales seem to be a comparatively old clade containing exclusively the obligate biotrophic white blister rusts (Thines and Voglmayr 2009), the Peronosporales, in addition to the obligate biotrophic downy mildews, comprise also several saprotrophic, necrotrophic and hemibiotrophic genera, e.g., *Salisapilia*, *Pythium*, and *Phytophthora* (Beakes et al. 2012; Hulvey et al. 2010; Runge et al. 2011b; Thines 2014). The downy mildews make up more than one third of the known oomycete species, with the largest oomycete genus, *Peronospora*, containing about 400 described species (Constantinescu 1991). The downy mildews are believed to have arisen from *Phytophthora*-like ancestors and were shown to be embedded within this genus (Göker et al. 2007; Runge et al. 2011b; Thines 2009; Thines et al. 2009b). However phylogenomic investigations with a limited taxon sampling seem to favor an independent evolution of *Phytophthora* and downy mildews (Matari and Blair 2014; Seidl et al. 2011), or their polyphyly (Sharma et al. 2015). In any case, the downy mildews and *Phytophthora* are closely related groups and share RxLR-type effectors as a synapomorphic trait (Baxter et al. 2010; Thines and Kamoun 2010). It is conceivable that the advent of these effectors, which seem to be efficiently taken up by host cells, were the landmark in the evolutionary success of this group. Due to an increasing specialization to biotrophic plant pathogenicity, the necrotrophic and saprophytic phases became less important and less efficient, allowing the loss of major energy-consuming metabolic pathways, ultimately leading to obligate biotrophy. Indeed, downy mildews seem to lack the capacity to reduce inorganic nitrogen and sulfur

(Baxter et al. 2010). In addition, other pathways have also been lost, such as the de novo synthesis of sterols (Beakes et al. 2012; Dick 2001). Whether downy mildews are monophyletic or polyphyletic has not been fully resolved, even though there is some evidence for monophyly (Göker et al. 2007; Runge et al. 2011b). However, until all genera of downy mildews have been included in multigene phylogenies with a reasonable and representative taxon sampling, this cannot be considered certainty. A phylogenetic hypothesis for the Peronosporales is given in Figure 1. Additional comprehensive reference listings on *Peronospora* evolution, and other topics covered below in this review, are included in Supplementary File S1.

AN OVERVIEW OF THE DOWNY MILDEW GENERA

So far 19 downy mildew genera have been described. Most of the species and genera are present in three major monophyletic groups, which harbor more than 700 species. These groups are the downy mildews with colored conidia (*Peronospora* and *Pseudoperonospora*), the downy mildews with pyriform haustoria (*Basidiophora*, *Benua*, *Bremia*, *Novotelnova*, *Paraperonospora*, *Plasmopara*, *Plasmoverna*, and *Protobremia*), and the brassicolous downy mildews (*Hyaloperonospora* and *Perofascia*). Apart from these, several grass-parasitic downy mildew genera have been described, of which the graminicolous downy mildews with lasting sporangiophores (*Graminivora*, *Poakateshia*, and *Viennotia*) seem to be monophyletic. The phylogenetic affinities of the remaining genera (*Eraphthora*, *Peronosclerospora*, *Sclerophthora*, and *Sclerospora*) are less clear, but *Eraphthora* and *Sclerophthora* seem to be related and in some phylogenies *Peronosclerospora* and *Sclerospora* are also grouped (Thines et al. 2008), even though support for this is

FIGURE 1

Schematic overview on the phylogeny of the Peronosporomycetes. Numbers in boxes are approximate species numbers.

generally low. The phylogenetic relationships of the three major downy mildew groups and the graminicolous lineages remain unclear, suggesting rapid evolution when biotrophy evolved.

Of the downy mildew groups, especially the graminicolous downy mildews (GDM) remain enigmatic. Apart from *Peronosclerospora*, all GDM genera are currently considered to be monotypic, and two of the genera, *Poakatesthia* and *Viennotia*, are only known from the type collection (Göker et al. 2003; Thines et al. 2007). Despite containing less than 20 species, GDM have the widest spectrum of morphological features, as they contain both species with lasting (*Graminivora*, *Poakatesthia*, and *Viennotia*) and evanescent (*Eraphthora*, *Peronosclerospora*, *Sclerophthora*, and *Sclerospora*) sporangiophores. Some genera have traits either unique among downy mildews, such as intracellular mycelium in *Poakatesthia* (Thines et al. 2007), indeterminate sporangiophore growth in *Viennotia* (Göker et al. 2003), or closely resemble eudicot downy mildew genera, such as *Basidiophora*, *Bremia*, or *Plasmopara* (for review see Thines 2014). Only the genus *Peronosclerospora* has been widely investigated during the past two decades (Bock et al. 1999; Magarey 2004; Perumal et al. 2006; Shivas et al. 2012; Telle et al. 2011; Thines et al. 2008), mainly because it contains several pathogens that are considered quarantine pests, due to their pathogenicity to maize (Kenneth 1981; Shaw 1975, 1976; Shivas et al. 2012; Telle et al. 2011). GDM diversity is largely unexplored, in contrast to other downy mildew groups; they are a paleotropical element and only few occur on economically important crops. It is noteworthy that while it is known that maize is highly susceptible to species of that genus (Kenneth 1981; Shivas et al. 2012; Telle et al. 2011), there are several cases where a *Peronosclerospora* species is only known from the alien host, maize, but not from the natural host in the same area (Shivas et al. 2012; Telle et al. 2011).

The third largest group of downy mildews, which is mostly restricted to one plant family, are the brassicolous downy mildews (BDM), even though a few species of this group are parasitic to other plant families, such as Capparaceae, Resedaceae, Limnanthaceae, Cistaceae, and Zygophyllaceae (Constantinescu and Fatehi 2002; Göker et al. 2009b). The BDM contain about 100 known species (Constantinescu 1991), but there are several species-level clades which have not yet been formally described (Göker et al. 2009b). Importantly, it also includes an economically relevant but yet undescribed species occurring on arugula (or rocket; *Eruca sativa*). Without quarantine regulations in effect, it is fast-spreading throughout the world (Göker et al. 2009b; Koike 1998). The BDM contain two genera, *Hyaloperonospora* and *Perofascia*, of which the monotypic genus *Perofascia* is characterized by sporangiophores that often intertwine, thick-walled oospores, and hyphal haustoria. The genus seems to be restricted to the Brassicaceae tribe Lepidieae (Constantinescu and Fatehi 2002). On plants belonging to the same tribe, but also on plants of about 20 other tribes of Brassicaceae, the genus *Hyaloperonospora* can be found. *Hyaloperonospora* is characterized by tree-like sporangiophores, comparatively thin-walled oospores, and globose to lobate haustoria. Like *Perofascia*, this genus was segregated from *Peronospora* only after molecular phylogenetic analyses were able to prove distinctiveness from *Peronospora* (Constantinescu and Fatehi 2002; Riethmüller et al. 2002; Voglmayr 2003), rendering them the first two downy mildew genera described with the aid of molecular phylogenies. The genus *Hyaloperonospora* is the third largest genus of downy mildews, containing more than 100 species, which can infect economically important Brassicaceae crops, e.g., horseradish (*Armoracia rusticana*), mustard greens (*Brassica juncea*), rapeseed (*B. napus*), cabbage (*B. oleracea*), Chinese cabbage (*B. rapa*), arugula (*Eruca sativa*), wasabi (*Eutrema japonicum*), watercress (*Nasturtium officinale*), and radish (*Raphanus sativus*). The downy mildew of *Arabidopsis thaliana*, *Hyaloperonospora arabidopsidis* (Göker et al. 2009b) has become a model organism to dissect plant-pathogen interactions

(Baxter et al. 2010; Coates and Beynon 2010). The BDM have been monographed by Gäumann (1918) and this almost 100-year-old work is still the most important source of reference for this group, together with the list of downy mildew names at that time placed in *Peronospora* by Constantinescu (1991). Since this last monograph, only few new species of this genus have been published (Voglmayr et al. 2014a), despite the fact that numerous new species-level clades have been found in phylogenetic analyses (Göker et al. 2009b).

The downy mildews with pyriform haustoria (DMPH) are morphologically diverse in terms of their sporangiophores, yet united by all producing small pyriform haustoria. The group currently comprises eight genera (*Basidiophora*, *Benua*, *Bremia*, *Novotelnovia*, *Paraperonospora*, *Plasmopara*, *Plasmoverna*, and *Protobremia*). Apart from the genera *Plasmopara* and *Plasmoverna*, all genera in this group are restricted to Asteraceae. *Plasmoverna* is restricted to Ranunculaceae (Constantinescu et al. 2005), while *Plasmopara* has a wide host spectrum in eudicots (Palti and Kenneth 1981). The genera *Bremia*, *Novotelnovia*, and *Protobremia* are closely related and united by the more or less regular aggregation of ultimate branchlets at the sporangiophore tips. Also in phylogenetic investigations (Thines et al. 2008, 2010; Voglmayr et al. 2004), these genera are closely related and more accessions of the genera *Bremia* and *Plasmopara* need to be included in multigene phylogenies to investigate if they are sufficiently distinct from each other in order to be retained. The genera *Novotelnovia* and *Protobremia* are monotypic and are only known from the host genera *Scorzonera* and *Tragopogon*, respectively. In contrast, the genus *Bremia* is diverse (Choi et al. 2011; Thines et al. 2010; Voglmayr et al. 2004) and contains several distinct species, including the causal agent of lettuce downy mildew, *Bremia lactucae*. The genus *Benua* is monotypic and possesses stout unbranched sporangiophores half-immersed in the stomata openings of its only known host, *Cyclachaena xanthiifolia* (Constantinescu 1998). Since a detailed revision of an earlier monograph by Constantinescu (1998) the genus *Basidiophora*, which affects solely members of the tribe Astereae, was believed to be monotypic, until recent phylogenetic investigations showed that several distinct species-level clades are present in this genus ((Sökücü and Thines 2014). Due to its often inconspicuous symptoms, it seems possible that downy mildew caused by *Basidiophora* is often overlooked and that this genus occurs on a wider range of Astereae than known until now. The genus *Paraperonospora* contains species parasitic to members of the tribe Anthemideae. Only two of its species have been included in phylogenetic investigations so far. *Paraperonospora* groups together with *Bremia*, *Novotelnovia*, and *Protobremia* (Göker et al. 2007). As a synapomorphy of this group, sporangiophore branches are widening toward the ramifications. This feature is easily seen in *Paraperonospora* (Constantinescu 1989), but less obvious in some species of *Bremia*. *Plasmoverna* is the only member of the DMPH that does not have hosts in Asteraceae. It is characterized by comparatively stout, irregularly branched sporangiophores with usually wide, tube-like ultimate branchlets (Constantinescu et al. 2005). Previously all members of this group had been subsumed under *Plasmopara pygmaea*, but both morphological and phylogenetic investigations show that several distinct species exist in this group (Constantinescu et al. 2005; Voglmayr et al. 2004). The genus *Plasmopara* is the second largest genus of downy mildews, with about 150 species. These occur on a broad range of taxa, in particular on asterids, but also on rosids. Only a minor part of the known species have so far been included in detailed phylogenetic investigations (Thines 2007b; Voglmayr et al. 2004), and thus evolutionary patterns in this genus remain obscure. Similar to the other genera with pyriform haustoria *Plasmopara* species carry several large repeat elements in their ITS2 region (Thines 2007a, b), which complicated the use of ITS as a barcoding region. As a consequence, *cox2* mtDNA has been recommended as

barcoding locus for oomycetes, because it has widely been used in previous phylogenetic analyses of diverse oomycete genera, including DMPH (Choi et al. (2015a) and references therein).

The largest group of downy mildews comprises the downy mildews with colored conidia (DMCC), and is made up by the two genera *Peronospora* and *Pseudoperonospora*. Both genera feature purplish gray to blackish sporangia, which germinate with zoospores in case of the genus *Pseudoperonospora* (Waterhouse and Brothers 1981), but with a germ-tube in the genus *Peronospora* (Byford 1981). None of the reports that sporangia of members of the genus *Peronospora* could germinate via zoospores (Berkeley 1862) could be confirmed so far, but for *Pseudoperonospora* it is also known that sporangia may germinate with germ-tubes. The genus *Pseudoperonospora* mostly affects hosts in Rosids, in particular Urticales, but also Meliaceae, Balsaminaceae (Voglmayr et al. 2009), and Cucurbitaceae (Waterhouse and Brothers 1981) have been reported as hosts. However, *Pseudoperonospora puertoricensis* has not yet been included in molecular phylogenetic studies and there is only a single report on *Impatiens irwingii* of the Balsaminaceae (Voglmayr et al. 2009). Interestingly, the causal agent on *impatiens* was identified as *Pseudoperonospora cubensis* (Voglmayr et al. 2009), a broad host range pathogen of Cucurbitaceae (Runge et al. 2011a; Runge and Thines 2011, 2012), which apparently jumped from Cannabaceae to the rather distant Cucurbitaceae and further to Balsaminaceae. However, as there have so far not been any further reports of *Pseudoperonospora* on Balsaminaceae, the presence on this family is probably adventitious. As mentioned before, the genus *Peronospora* is by far the largest genus of Peronosporaceae and its hosts are found across the whole range of eudicots as well as on Alliaceae and reportedly Liliaceae of the monocots (Constantinescu 1991). The evolutionary success of the DMCC is probably due to the evolution of melanized sporangia, which might enable a longer survival under solar radiation and during long range transport by wind currents (Cohen and Rotem 1971; Hildebrand and Sutton 1982; Lebeda and Schwinn 1994). Less than one fifth of the known species of *Peronospora* have been included in molecular phylogenies so far (Belbahri et al. 2005; Choi et al. 2007a, 2007b; Choi et al. 2009; García-Blázquez et al. 2008; Thines et al. 2009a; Voglmayr 2003; Voglmayr et al. 2014b), but it seems that after the removal of *Paraperonospora* (Constantinescu 1989), *Perofascia*, and *Hyaloperonospora* (Constantinescu and Fatehi 2002) the genus is now monophyletic. An overview on the diversity of downy mildews is given in Figure 2.

BROAD AND NARROW SPECIES CONCEPTS

With respect to species concepts in downy mildews and in particular in the genus *Peronospora* there have long been two conflicting views—the narrow species concept, advocated by Gäumann (1918, 1923) and Gustavsson (1959), and the broad species concept advocated by de Bary (1863) and Yerkes and Shaw (1959). While the narrow species concept was followed by most taxonomists, the broad species concept, which ascribed the host specificity of some downy mildew pathogens to specialized forms (*formae speciales*) of the same species, was mostly followed by applied plant pathologists. This schism made the sequencing of the *Arabidopsis* downy mildew seem to be of direct importance to plant pathologists working on economically important Brassicaceae crops. However, due to the fact that the downy mildew species are only distantly related, even though the genome of *Hyaloperonospora arabidopsidis* has provided important insights into downy mildew evolution (Baxter et al. 2010), the findings are difficult to translate into applications in *Brassica* crops. In general, molecular phylogenetic analyses have provided solid evidence for a high degree of specialization for most downy mildew species, also including the genera *Hyaloperonospora* (Göker et al. 2009b; Voglmayr et al. 2014a) and *Peronospora* (Belbahri et al. 2005; Choi et al. 2007b, 2008, 2009, 2010, 2015b;

Thines et al. 2009a; Voglmayr et al. 2014b). There are only rare exceptions—a few downy mildew species seem to have broad host ranges (Kenneth 1981; Runge et al. 2011a). However, in line with molecular phylogenetics, infection trials have shown that downy mildews are generally highly host specific (Byford 1967; Gäumann 1919, 1923; Lebeda and Syrovátko 1988; Sherriff and Lucas 1990). Thus it seems reasonable to treat emerging downy mildew diseases on new hosts as separate species—especially with respect to quarantine—until infection trials and phylogenetic investigations have revealed whether or not they are highly host specific. Had this been done in the past, it might have been possible to restrict pandemic downy mildew agents, such as *Peronospora belbahrii* from sweet basil, *Peronospora somniferi* from opium poppy, *Peronospora salviae-officinale* from sages, and *Plasmopara obducens* s.l. from cultivated *Impatiens* species, preventing high yield losses around the world (see below).

DIVERSITY PATTERNS IN PERONOSPORA

As the amount of species in the genus *Peronospora* is high, there have been attempts to subdivide the genus into subgenera, sections or series in the 19th century (de Bary 1863; Fischer 1892; Schröter 1886, 1889). de Bary (1863) divided the genus into four sections, viz., *Zoosporiparae* (now, mostly belonging to *Phytophthora* or *Plasmopara*), *Plasmatoparae* (to *Plasmopara* or *Plasmoverna*), *Acroblastae* (to *Bremia*), and *Pleuroblastae* (to *Peronospora* and allied genera). Later Schröter (1889) limited *Peronospora* to the latter section. Based mostly on oospore features, Fischer (1892) and Schröter (1889) distinguished two sections in this genus, namely *Leiothecae* and *Calothecae*, for which a further division into smaller groups was made (Fischer 1892; Gäumann 1923; Schröter 1889; Skalický 1966). After the genera *Plasmopara* (Schröter 1886) and *Pseudoperonospora* (Rostovtzev 1903) were split from *Peronospora*, the genus *Peronospora* was usually considered to include all nonpapillate downy mildew species. Parts of the different groups were later described as genera of their own because of apparent differences in morphology, which are in line with a phylogenetic placement outside the DMCC. These genera are *Paraperonospora* (Constantinescu 1989), *Hyaloperonospora* and *Perofascia* (Constantinescu and Fatehi 2002), which were previously placed in two groups, *Effusae* and *Parasiticae*, of *Peronospora* (de Bary 1863; Gäumann 1923). The different subgroups of *Peronospora* are not widely used anymore, as several do not seem to be monophyletic and the placement of some species seems ambiguous.

Currently, there is no multigene phylogeny available for *Peronospora* with a representative amount of species from the different subgroups, but phylogenetic investigations have rather focused on specific groups to resolve specific taxonomic problems, e.g., of the *Peronospora arborescens* complex (Voglmayr et al. 2014b) and the *Peronospora farinosa* complex (Choi et al. 2015b). Thus, the only phylogeny of *Peronospora* with a representative taxon sampling available is based on ITS sequences (Voglmayr 2003), leaving most basal nodes in the genus unresolved. Some groups, however, received some statistical support in ITS-based phylogenies. Among these groups are the pathogens of core Fabaceae (García-Blázquez et al. 2008; Riethmüller et al. 2002; Voglmayr 2003), even though it remains unclear if all downy mildew pathogens of Fabaceae form a monophylum. Also for the pathogens of Rosaceae (Choi et al. 2007a; Göker et al. 2009b; Voglmayr 2003) it seems possible that they are either monophyletic or paraphyletic at the base of the genus. Pathogens of Ranunculaceae might be monophyletic and are placed in a larger clade comprising mainly members of the order Caryophyllales, but also of unrelated families, such as Solanaceae and Alliaceae (Voglmayr 2003). Pathogens of Lamiales seem to be restricted to one clade, but Plantaginaceae seem to have been colonized twice independently (Y.-J. Choi and M. Thines, unpublished data). Similarly, Papaveraceae and Polygonaceae seem

to have been colonized at least two times independently. Overall, it seems that host jumping has been an important factor in the evolution of *Peronospora* on different scales, because within the groups restricted to a certain host family, e.g., on Fabaceae (García-Blázquez et al. 2008), host and pathogen phylogenies are not congruent. Thus, it can be assumed that unknown innovation within a certain group of pathogens enabled the jump to and diversification on a new group of hosts several times. This is apparent from the floricolous downy mildews, which seem to represent a monophyletic assemblage (Thines and Kummer 2013; Voglmayr 2003), and probably evolved organ-specific effectors and mechanisms that also enable some restriction of sporulation to floral tissues. Even though the floricolous species are closely related, they colonize hosts belonging to three different orders—Asterales, Dipsacales, and Lamiales (Thines and Kummer 2013).

Probably the most noteworthy host jump happened in the clade predominantly parasitic to Caryophyllales. In this group, a host jump from dicots to the family Alliaceae of the monocots has occurred (Voglmayr 2003). This host jump has not yet led to a large-scale radiation in this family and the genetic distance from

some pathogens of Chenopodiaceae is rather low, so it could be assumed that the host jump has occurred in evolutionary recent times. This situation is similar to the host jump across orders in *Pseudoperonospora*, even though *Pseudoperonospora cubensis* has been able to radiate to a wide range of Cucurbitaceae, becoming one of the very few downy mildews with a broad host range (Runge et al. 2011a; Runge and Thines 2011, 2012; Voglmayr et al. 2009).

Like in *Plasmopara*, which includes hosts in a great variety of Angiosperms, it is unclear which host family the genus *Peronospora* evolved from. As *Pseudoperonospora* seems to have evolved in Rosales and since several basal clades in *Peronospora* are from this group (Göker et al. 2007, 2009a; Voglmayr 2003), it is possible that the DMCC in general have started their host jumping and radiation from hosts in this order.

AN OVERVIEW OF IMPORTANT *PERONOSPORA* SPECIES—WHAT WE KNOW

***Peronospora belbahrii*: Downy mildew of sweet basil.** In 2002 basil downy mildew was reported in Europe for the first time

FIGURE 2

Overview on the symptoms and morphology of various downy mildews. First column shows upper leaf surface, second column shows the lower leaf surface of the infected leaves, the third and fourth columns show sporangiophores, and fifth column shows ultimate branchlets (upper picture in each row) and conidia (lower pictures in each row). **A**, *Plasmopara obducens* s.l., **B**, *Hyaloperonospora brassicae* s.l., **C**, *Peronospora belbahrii*, **D**, *Peronospora manshurica*, **E**, *Peronospora schachtii*, and **F**, *Peronospora variabilis*. Bars equal 100 μ m for conidiophores and 20 μ m in ultimate branchlets and conidia.

(Belbahri et al. 2005). Adopting a broad species concept, the downy mildew was first referred to as *Peronospora lamii*, but often referred to as simply a *Peronospora* sp. (Belbahri et al. 2005). After the initial reports from Switzerland, France, and Italy (Belbahri et al. 2005), the pathogen was soon found in other European countries (Thines et al. 2009a) before making its way to North America and West Asia. Currently the pathogen is found in almost all areas around the world where basil is cultivated (Farr and Rossman 2015). Most likely the pathogen was spread by infected seeds (Belbahri et al. 2005), similar to other seedborne *Peronospora* species. The potential seedborne nature of *Peronospora* species carries a great risk of spreading the pathogens by seed-trade, and import-restrictions may have halted *Peronospora belbahrii*. However, as initially a broad species concept had been assumed, appropriate regulations were not put in effect, resulting in the current pandemic occurrence of basil downy mildew. Molecular phylogenetic studies (Belbahri et al. 2005; Thines et al. 2009a) have shown that the basil downy mildew pathogen is different from both *Peronospora lamii* and *Peronospora swinglei* and detailed morphological investigations finally resulted in the description of a distinct species, *Peronospora belbahrii* (Thines et al. 2009a). Similarly the downy mildew on economically important sage species are neither caused by *Peronospora lamii* (Holcomb 2000; Yin and Yang 1998) nor *Peronospora swinglei* (Kochman and Majewski 1970; Müller and Kokes 2008; Shin and Choi 2006) as initially assumed, but by the specialized species, *Peronospora salviae-officinalis* and *Peronospora salviae-plebeiae* (Choi et al. 2009). The widespread nature of the diseases on basil and sage is also one of the few cases where a disease was noticed by the general public before the causal agent was even scientifically described.

***Peronospora destructor*: Downy mildew of onion.** As mentioned previously, *Peronospora destructor* arose from a host jump to Alliaceae, most likely from hosts in Chenopodiaceae. When this host jump occurred is unclear, but in evolutionary terms it seems to have been rather recent. *Peronospora destructor* was first described from onions in Britain, but is now widespread throughout nearly all countries where this crop is cultivated (Farr and Rossman 2015; Gustavsson 1959). *Peronospora destructor* is often fully systemic (Palti 1989), but secondary infections on foliage are also observed. The disease is primarily present on *Allium cepa*, but has also been reported on *Allium fistulosum*, *A. porrum*, and *A. schoenoprasum*, even though much less frequent (Farr and Rossman 2015; Gustavsson 1959). In addition, *A. tuberosum* is an economically relevant host crop of this pathogen in East Asia, e.g., China, Japan, and Korea. The disease is especially severe in cool and moist conditions and thus is one of the major diseases of onion in Northern Europe (Gustavsson 1959) and North America (Miller and Amador 1985; Smith et al. 1985). Genes conferring resistance to *Peronospora destructor* have been identified (Devries et al. 1992), but additional sources of resistance genes might be necessary to efficiently control the pathogen, especially as resistance against major fungicides exists in the pathogen population (Wright 2004). In addition to *Peronospora destructor*, there is only one other *Peronospora* species known to infect monocots, which was reported to occur on *Lilium candidum* in Russia (Stenina 1968). However, *Peronospora lilii* (as it was named) is a doubtful taxon, as the type is preserved only as a microscopic slide, without any fungus in the specimen capsule, and there is no further collection on this common host plant (Constantinescu 1991). In addition, the morphology of *Peronospora lilii* is quite similar to *Peronospora destructor*. It also might seem possible that a misidentification of a species of *Allium* as *Lilium candidum* had taken place, as plants of the genera, *Lilium* and *Allium*, can look similar at their young stages. *Peronospora lilii* has not yet been included in molecular phylogenies, so it remains unclear, whether this species resulted from an independent host jump to monocots or is related to (or conspecific with) *Peronospora destructor*.

***Peronospora effusa*: Downy mildew of spinach.** *Peronospora effusa* is one of the most important diseases of cultivated spinach (Byford 1981) and was first reported in Britain (Greville 1824). Similar to several other downy mildews of Chenopodiaceae, *Peronospora effusa* is often systemic and seed transmitted (Raabe and Pound 1952). Oospores have been found in commercial seed lots and it can be assumed that the pathogen was spread throughout the world with contaminated seeds. *Peronospora effusa* has been especially destructive in California (Feng et al. 2011; Klosterman et al. 2014), one of the main growing areas for spinach. Some race-specific resistance genes for *Peronospora effusa* have been identified in spinach (Feng et al. 2011; Satou et al. 2006), but many widespread cultivars are susceptible to the disease. *Peronospora effusa* is spread by wind currents (Klosterman et al. 2014) and thus inoculum can spread over large areas after sporulation occurs on systemically infected plants early in the season. However, the pathogen can also be detected using spore traps (Klosterman et al. 2014), enabling an early recognition in routine monitoring. Spinach downy mildew can be controlled using various fungicides (Koike et al. 1992), but a widespread application might lead to field resistance, similar to the situation in other downy mildew pathogens, so treatments should be evaluated carefully. Especially seed treatments might be useful in controlling this potentially devastating pathogen. Similar to other downy mildew species on Chenopodiaceae, *Peronospora effusa* was often regarded as a synonym of *Peronospora farinosa* (Yerkes and Shaw 1959), and as a result, many studies erroneously referred to spinach downy mildew as *Peronospora farinosa* (or *Peronospora farinosa* f. sp. *spinaciae*) (Feng et al. 2011). However, *Peronospora farinosa* has been described from the unrelated genus *Atriplex* (Constantinescu 1991; Fries 1832; Gustavsson 1959) and in addition is a dubious name proposed for rejection (Choi and Thines 2014). Thus, the name *Peronospora effusa* should be used for the causal agent of spinach downy mildew.

***Peronospora farinosa*: A phantom species.** *Botrytis farinosa*, the basionym of *Peronospora farinosa* was described by Fries (1832) as a pathogen of an undetermined *Atriplex* species from Sweden. However, the description seems to comprise multiple organisms, for example swimming spores were reported that are not present in *Peronospora* species and also the description of the sporangiophores has insufficient detail to clarify if a species of *Peronospora* was involved in the initial description. Furthermore, it is impossible to investigate the presence of *Peronospora* on a potential type specimen as no collection of the pathogen of Fries seems to be extant. As a consequence, the name *Botrytis farinosa* has been proposed for rejection (Choi and Thines 2014). In any case, the pathogens on *Atriplex*, which have been described as *Peronospora atriplicis-hastatae* (Săvulescu and Rayss 1932), *Peronospora litoralis* (Gäumann 1919), and *Peronospora minor*, are unrelated to the economically important pathogens of Chenopodiaceae. Among the economically important *Peronospora* affecting the Chenopodiaceae, molecular phylogenetic investigations have shown that these should be referred to as *Peronospora effusa* for the downy mildew pathogen affecting spinach (Choi et al. 2007b; Choi and Thines 2014), *Peronospora schachtii* for the *Peronospora* pathogen of beet (Choi et al. 2015b) and *Peronospora variabilis* for the causal agent of quinoa down mildew (Choi et al. 2010). Species of *Peronospora* on Chenopodiaceae and Caryophyllales, in general, seem to be highly host specific, as deduced from both infection trials (Gäumann 1919, 1923; Byford 1967) and phylogenetic investigations (Choi et al. 2007b, 2008, 2010, 2015b; Voglmayr 2003). This supports that *Peronospora* species occurring on weedy hosts of the Chenopodiaceae will mostly not be a threat for chenopodiaceous crops unless very closely related, with the exception of *Peronospora variabilis* which seems to affect both the weed *Chenopodium album* and the crop *Chenopodium quinoa* (Choi et al. 2010).

***Peronospora schachtii*: Downy mildew of sugar beet and Swiss chard.** *Peronospora schachtii* is widespread due to human activity, similar to other downy mildews on chenopodiaceous crops, and can be found in most areas in which sugar beet or Swiss chard are grown commercially. Similar to spinach, the beet crop originates from Western and Central Asia and also in their natural range, downy mildew disease is common (Byford 1981; Farr and Rossman 2015). *Peronospora schachtii* seems to be highly specific to beet and no host outside this genus is currently known (Byford 1967). Similar to the situation with *Peronospora effusa* and *Peronospora variabilis*, *Peronospora schachtii* has been referred to as *Peronospora farinosa* (or *Peronospora farinosa* f. sp. *betae*) in the past (Byford 1981; García-Blázquez et al. 2006), which is a dubious name for a pathogen of *Atriplex* (Choi and Thines 2014; Constantinescu 1991; Fries 1832) largely unrelated to the various species infecting crops in Chenopodiaceae (Choi et al. 2007b, 2015b). *Peronospora schachtii* often grows systemically to infect beet tubers (Byford 1981), with which the pathogen can be transmitted. In addition, the pathogen is also seedborne, resulting in a high risk of distributing the pathogen by seed trade. The impact of *Peronospora schachtii* on the production of sugar beet and Swiss chard differs within different growing areas, but similar to other downy mildew pathogens, cool and moist conditions seem to favor disease development. The disease can be controlled with fungicides, but like in other downy mildews, resistance to major classes of fungicides is known.

***Peronospora somniferi*: Downy mildew of opium poppy.** Downy mildew on opium poppy had been attributed mainly to *Peronospora arborescens* (Landa et al. 2007; Montes-Borrego et al. 2008; Yossifovitch 1929) before detailed phylogenetic investigations became available. However, it soon became apparent that downy mildew disease on opium poppy is caused by at least two distinct species of *Peronospora* (Landa et al. 2007). Thorough morphological and molecular phylogenetic investigations, including the type host of *Peronospora arborescens*, revealed that this species does not cause downy mildew on opium poppy but another species, *Peronospora somniferi* was involved instead (Voglmayr et al. 2014b). On a global scale, two different *Peronospora* species, *Peronospora meconopsidis* and *Peronospora somniferi*, are economically relevant, the latter of which seems to be more widespread (Voglmayr et al. 2014b). For *Peronospora somniferi* its widespread occurrence is believed to be attributed to seed trade (Landa et al. 2007). This also seems to be the case for *Peronospora meconopsidis*, considering its systemic nature. Due to its potentially devastating effects on opium poppy, the pathogen was also suggested to be a candidate bioweapon to fight communities depending on the crop. Research into the control of the pathogen is rather at its infancy and both the resistance of the plant to the pathogen as well as the resistance structure of the pathogen toward fungicides are not well studied.

***Peronospora sparsa*: Downy mildew of roses.** *Peronospora sparsa* is an important pathogen of rose (Gomez 2013), but has also been reported from raspberry and blackberry species (*Rubus* spp.) (Koponen et al. 2000; Lindqvist et al. 1998; Rebollar-Alviter et al. 2009). The pathogen was first described in England (Berkeley 1862) but occurs in most areas in which roses are commercially grown. As its symptoms are often not typical for downy mildew (Berkeley 1862; Gomez 2013) and sporulation is usually sparse—as the name already suggests—the pathogen is probably frequently overlooked or misidentified. There has been much debate regarding the host specificities of two close species, *Peronospora sparsa* on roses and *Peronospora rubi* on species of the genus *Rubus* (Breese et al. 1991, 1994). While some studies suggested a rather broad host range for *Peronospora sparsa*, including brambleberry (Breese et al. 1991, 1994), other studies came to the conclusion that two distinct species exist on these hosts (Koponen et al. 2000). Molecular phylogenetic investigations also revealed an uncertain species delimitation (Choi et al. 2007a; Riethmüller et al. 2002;

Voglmayr 2003;) due to the relatively small number of taxa and genes analyzed, but infection trials have shown that at least under artificial conditions, the host range of *Peronospora sparsa* includes hosts apart from the genus *Rosa* (Breese et al. 1991, 1994). Most rose cultivars are susceptible to this pathogen (Schulz and Debener 2009), but resistance to downy mildew is not amongst the most important traits of interest to breeders, even though *Peronospora sparsa* is difficult to control with fungicides (Hukkanen et al. 2008). It is unclear, if rose downy mildew is seedborne, but the pathogen can be easily distributed with infected plants (Xu and Pettitt 2004).

***Peronospora tabacina*: Downy mildew of tobacco.** Tobacco continues to be a major crop in the United States and other parts of the world, despite the known potential harm of smoking to human health. One of its major pathogens is *Peronospora tabacina*, which can be found in all major tobacco growing areas (Farr and Rossman 2015), except for Far East Asian countries, such as China at the peak of global tobacco production. The pathogen was first reported in the United States (Smith and McKenney 1921) and subsequently in Australia (Klinkowski and Schmiedeknecht 1960). As tobacco is not native to Australia, it is likely that tobacco blue mold originates from native tobacco species of North America. The pathogen is sometimes referred to as *Peronospora hyoscyami* f. sp. *tabacina* (Hall 1989; Shepherd 1970), but this designation is questionable, as Shepherd (1970) reported the conspecificity of *Peronospora hyoscyami* with *Peronospora tabacina*, but also found two morphologically distinct groups within his broad species, *Peronospora hyoscyami*, although he did not describe them as different taxa. Considering the high host specificity of this pathogen for different host plants (Skalický 1964) and the usually narrow specialization of downy mildews, the pathogen is thus probably better referred to as *Peronospora tabacina*. The downy mildew disease caused by this pathogen can be severe, leading to high economic losses. In the United States, *Peronospora tabacina* has been classified as a potential bioweapon (Leeson 2000), as it could severely affect its economy with respect to the tobacco industry. There are several wild tobacco species that can be infected with *Peronospora tabacina*, including the model plant, *Nicotiana benthamiana*. Resistance against the disease seems to be present in some desert species (Zhang and Zaitlin 2008), and this resistance could gain additional importance, as populations of *Peronospora tabacina* seem to develop a high proportion of resistant strains readily after repeated fungicide applications over a longer period of time (Delon 1992; Lea 1999). The pathogen is distributed by wind and suspected to be transported over long distance with air currents (Hall 1989). A seedborne nature of the pathogen is also likely, considering its ability to grow systemically (Blanco-Meneses and Ristaino 2011).

***Peronospora variabilis*: Downy mildew of quinoa and lamb's quarters.** *Peronospora variabilis* infects the Royal Inka crop quinoa and has become an economically important pathogen in quinoa production. The pathogen seems to be conspecific with *Peronospora variabilis* from the weed *Chenopodium album* (Choi et al. 2010), which is frequently infected by downy mildew throughout Europe. It thus seems possible that the observed presence on *Chenopodium quinoa* is the result of a host jump from the weed to the closely related crop. However, this hypothesis needs to be tested using detailed population genetic investigations and infection trials. As the disease is potentially seedborne, seeds from regions where the pathogen has been recorded should be traded with caution. Fungicide resistance does not seem to be widespread, but has already been reported even in the most resistant cultivars.

SOME ADDITIONAL NOTEWORTHY SPECIES

The list of other *Peronospora* species that are noteworthy is long, so only a small selection of pathogens can be mentioned here. These

are species that are either already of some economic importance or could turn into economically important pathogens, should more aggressive genotypes arise.

Peronospora arthurii is a pathogen of *Oenothera* species. It is frequent both in North America and Europe. Infections can be systemic and if infestations are severe, the ornamental value of the plants is low (Spooner 2013).

Peronospora arborescens is a pathogen of *Papaver rhoeas* and not conspecific with *Peronospora meconopsidis* and *Peronospora somniferi* of opium poppy (Voglmayr et al. 2014b). It occurs frequently in ornamental plantings throughout Europe (Farr and Rossman 2015). There seem to be several independent species affecting different *Papaver* spp. (Voglmayr et al. 2014b), and several of these have not been described scientifically.

Peronospora conglomerata is a pathogen of wild and ornamental *Geranium* plants (Farr and Rossman 2015). It is one of the most frequent *Peronospora* species throughout Europe. The downy mildew reports of *Peronospora conglomerata* probably cannot be attributed to just one species, however phylogenetic evidence for this is currently not available.

Peronospora dicentrae affects bleeding heart species and has been reported as a noteworthy pathogen from time to time (Constantinescu 1991; Farr and Rossman 2015). It affects the popular plant, *Dicentra spectabilis* (now, classified in the genus *Lamprocapnos*), and has so far been reported only in South Korea. This species is often identified as *Peronospora corydalis*, and even though *Peronospora dicentrae* was found to be closely related to other *Peronospora* species from Fumariaceae (Göker et al. 2009a; Voglmayr 2003), further phylogenetic investigations are necessary to clarify its status. Currently, the pathogen does not seem to be a major factor in the production of bleeding hearts.

Peronospora ficariae affecting *Ficaria verna* is probably the most widespread *Peronospora* species in Central Europe, along with *Peronospora aparines* on *Galium aparine*, *Peronospora alsinearum* on *Stellaria media*, and *Peronospora arvensis* on *Veronica hederifolia*. There are various reports of the pathogen on different ornamental Ranunculaceae species (Gäumann 1923; Gustavsson 1959; Constantinescu 1991) but given the high degree of host specificity in the species affecting Ranunculaceae (Gäumann 1923), it seems more likely that these reports have to be attributed to multiple different species.

The name *Peronospora grisea* is often used to refer to downy mildew pathogens affecting members of the former Scrophulariaceae, especially downy mildew agents on several species of *Hebe* and *Veronica* (Farr and Rossman 2015). However, this name should only be applied to the pathogen on *Veronica beccabunga*, a semi-aquatic *Veronica* species from which the pathogen was originally described. There are several independent phylogenetic lineages of *Peronospora* affecting *Veronica* and related genera, most of which have not been described, yet. This also includes the economically relevant downy mildew of *Hebe buxifolia* (Y. J. Choi and M. Thines, unpublished data).

Peronospora lini is a rare pathogen of *Linum catharticum* in Central Europe (Müller and Kokes 2008) and *Linum sulcatum* in North America (Constantinescu 1991; Farr and Rossman 2015). The pathogen seems to be extremely rare on cultivated flax. As the symptoms are rather inconspicuous (Schröter 1876), it seems possible that the pathogen is much more widespread.

Peronospora manshurica is a pathogen causing downy mildew on soybeans. Even though it has been observed in several parts of the world it usually does not incite economically relevant losses.

Peronospora oertelina is a pathogen of *Primula* species (Kühn 1884). It is present along with its host throughout Europe (Farr and Rossman 2015), but is probably often overlooked because of its rather inconspicuous symptoms. The pathogen currently does not seem to be of importance in the production of *Primula* for ornamental purposes.

Peronospora plantaginis and *Peronospora alta* are distinct pathogens (Shin and Choi 2006; Wilson 1914) reported to be affecting *Plantago* species, including the medicinal plant, *Plantago lanceolata*, which is grown commercially in Europe. *Peronospora alta* is common in *Plantago major*, but the status of the pathogen affecting *Plantago lanceolata* is unclear. It was classified as *Peronospora lanceolata*, an invalid name (Constantinescu 1991). Detailed phylogenetic and morphological investigations are necessary to disentangle the *Peronospora* lineages affecting the genus *Plantago*.

Peronospora radii is a floricolous downy mildew affecting the flowers and sometimes leaves of cultivated *Chrysanthemum* species (Ben-Ze'ev et al. 1987; Gustavsson 1959; Koike et al. 2004), but can also affect wild members of the tribe Anthemideae (Ben-Ze'ev et al. 1987). Even though the pathogen can cause economically relevant losses it does not seem to pose a major threat to *Chrysanthemum* production, at present.

Peronospora stigmaticola is a floricolous pathogen, which predominantly sporulates on the stigmata of mint plants (Thines and Kummer 2013). Because of its floricolous nature, the pathogen is easily overlooked and it is unclear, to which degree it is present in commercially grown mints.

POTENTIAL EMERGING PERONOSPORA DISEASES

Peronospora diseases cause high economic losses each year. During the past two decades several new *Peronospora* diseases have been emerging, e.g., *Peronospora belbahrii* on sweet basil (Belbahri et al. 2005; Landa et al. 2007; Thines et al. 2009a), *Peronospora salviae-officinalis* on sage (Choi et al. 2009; Thines et al. 2009a), and *Peronospora variabilis* on quinoa. However, there are additional emerging *Peronospora* species, which were only recently encountered and which might become economically important in the future.

Most importantly, this is *Peronospora* sp. currently devastating ornamental *Aquilegia* in Great Britain (Denton et al. 2015). The disease has been found in various botanical gardens in England and Wales (C. Thomas, personal communication) and seems to spread fast, as it is potentially seedborne and can also be distributed with infected plants. If no appropriate measures to restrict the pathogen are set into effect within a short period of time, it is conceivable that the pathogen will spread to other parts of Europe and eventually other regions around the world where *Aquilegia* is grown for ornamental purpose.

Also *Peronospora* sp. on *Eustoma* (Cunnington 2003), a widely grown ornamental of the Gentianaceae, has the potential to become a worldwide threat to the production of the host, as also this pathogen is often systemic and thus potentially seedborne and easily distributed.

Another pathogen of the genus *Peronospora* with the potential to become widespread is *Peronospora* sp. on *Phygellus* (Hall and Humphreys-Jones 1989), a popular ornamental in some parts of North America. It is unclear, if the pathogen can be spread with seeds, but a distribution with infected host plants by trade might have a similar effect.

WHAT WE KNOW WE DON'T KNOW

Several aspects regarding the biology and evolution of the genus *Peronospora* remain unknown. This includes the question of how many species of *Peronospora* exist. This question is difficult to answer for several reasons. First, there have been comparatively few researchers investigating downy mildews systematically over time, even though scholars such as de Bary (1863), Schröter (1886), Wilson (1914), Gäumann (1918, 1919, 1923), Gustavsson (1959), Novotelnova et al. (1979), Novotelnova and Pystina (1985), and Constantinescu (1989, 1998)—to name only a few—have devoted

a significant proportion of their work to studying downy mildews. In addition, several naturalists have amassed huge collections of plant pathogenic fungi, especially in the late 19th and early 20th century. However, their activity was mostly restricted to the temperate zones of Europe and North America. The knowledge from other parts of the world is thus fragmentary, some areas, especially in East Asia and Africa are vastly unexplored. The taxonomy of the species in Europe and North America is complicated by the often-applied broad species concepts (de Bary 1863; Yerkes and Shaw 1959). This might have discouraged the description of new species, even though it was shown by infection trials that only some are able to infect various hosts of the same genus, while others seem to be host-species-specific (Gäumann 1919, 1923; Sherriff and Lucas 1990). Molecular phylogenetic investigations suggest that the latter case seems to be more frequent, especially in the genus *Peronospora* (Belbahri et al. 2005; Choi et al. 2007a, 2007b, 2009; García-Blázquez et al. 2008; Thines et al. 2009a; Voglmayr 2003; Voglmayr et al. 2014b). Considering the many different host species from which *Peronospora* has been reported (Constantinescu 1991) and comparing this number with the about 300 species described from temperate Europe and North America, is suggestive of the possibility that these reports might equal about 800 species. In addition to this the knowledge of potential host plants for downy mildews is still incomplete, as each year several new hosts for *Peronospora* are reported, e.g., *Buddleja*, *Ranunculus asiaticus*, *Aquilegia* (Denton et al. 2015). Taking this into account the amount of *Peronospora* species in temperate Europe and North America can be estimated conservatively to about 1,000 to 1,500. Extrapolating this to other areas of the world for downy mildew genera in general is difficult, as downy mildew genera seem to have different centers of diversity. For example, *Plasmopara* seems to be most diverse in North America (Thines 2014), while *Bremia* is a predominantly European to Eurasian genus (Choi et al. 2011; Marlatt 1974; Thines 2014; Thines et al. 2010), and *Peronosclerospora* seems to have its highest diversity in South-East Asia (Spencer and Dick 2002). *Peronospora* is a widespread, primarily northern hemispheric genus, with a high diversity in families such as Fabaceae, Caryophyllaceae, Ranunculaceae, and Boraginaceae, which have a high diversity in Asia and the Mediterranean. Extrapolating from the temperate regions of Europe and North America to the rest of the world has to be fraught with some uncertainty, but it does not seem to far from hand to assume that a total of 3,000 to 5,000 species of *Peronospora* could exist, which would mean that only about 10% of the species of *Peronospora* have been described, yet.

Even less is known about the distribution ranges of downy mildews. Only for some major pathogens of crops, such as *Peronospora effusa*, *Peronospora destructor*, and *Peronospora tabacina*, sufficient records and reports exist to extrapolate their distribution range (Farr and Rossman 2015). However, the presence of these downy mildews is mostly due to human trade activity and agricultural practice and does not reflect natural distribution ranges of these pathogens. Thus, even for extremely common species, such as *Peronospora ficariae* or *Peronospora aparines* in Central Europe and *Peronospora arthuri* in North America no distribution maps are available. Several uncommon or easily overlooked species such as *Peronospora corollae* or *Peronospora stigmaticola* are collected only rarely, often only a few times since their discovery. Therefore, it is also vastly unknown if host and pathogen ranges are mostly congruent or if the pathogen is missing from some areas where the host is present. From the evolutionary perspective this would be an important piece of information, as a range extension of the host to escape the pathogen (which could be restricted by the survival of oospores), could be an important driver of plant evolution.

Another largely unexplored field linked to the previous one is how downy mildews persist in host populations. Of course it is known that many species of *Peronospora* produce oospores or can outlast in perennial tissue of their hosts (Inaba et al. 1982; Landa

et al. 2007; Xu and Pettitt 2004), and it is also known that several can be distributed together with seeds (Belbahri et al. 2005; Landa et al. 2007). But the importance for this for maintaining the pathogen populations is not known in detail and unknown for most species without economic relevance. This is also the case for the question how ephemeral or stable the presence of downy mildew disease in host populations would be. The finding of Constantinescu et al. (2005) that presumably the same host (meta-) population that Unger had sampled in the first half of the 19th century still had downy mildew infestation more than 150 years later suggests a rather stable equilibrium for some species. However, own observation show that there are probably rare cases in which after the occurrence of a pathogen the host population can be wiped out and a new population of the host settling later would be unaffected (M. Thines, *unpublished observations*). The contribution of asymptomatic infections to the persistence of downy mildews remains to be explored. Similar to the situation in *Albugo* (Ploch and Thines 2011), downy mildews can infect hosts systemically and be seed borne (Upadhyaya 1987). For the floricolous species of *Peronospora* it is known that most infected hosts will look like their uninfected counterparts until flowers develop (Thines and Kummer 2013), while other downy mildews can cause rather inconspicuous symptoms. Thus, it seems possible for *Peronospora* species that an asymptomatic vertical transmission could be an important factor in their epidemiology.

The question of how *Peronospora* diversified on its various hosts is not well understood. From the incongruence of pathogen and host phylogenies on several taxonomic levels, it can be deduced that host jumps have played an important role in the evolutionary history of the genus (Choi et al. 2015b; Voglmayr 2003). However, it is not known how long speciation processes would take in downy mildews and how frequently host jumps of longer host phylogenetic distance would take place. It is conceivable, however, that a host jump to a previously naïve group of hosts could open the possibility for extensive radiation, once effectors have become efficient in suppressing defense on that particular host group. As an onset of host–pathogen coevolution with the well-studied R-gene–Avr-gene interaction (Allen et al. 2004; Coates and Beynon 2010; McDowell and Simon 2006; Thines and Kamoun 2010) can be expected only after the pathogen has established itself well enough in the host population to exert a selection pressure, the initial colonization of a new host group can be expected to be primarily dependent on the evolution of effectors that overcome innate immunity, leaving the fine tuning to later evolutionary steps. This also means that after an initial radiation process to various hosts in the group to which the host belongs, and to which the host jump occurred, there will be a selection pressure to restrict the pathogen, which needs to be matched by pathogens. As these responses will be different in each host lineage, it can be expected that the counter-response will also not be by the complete pathogen populations, as too many simultaneous adaptations would be necessary. This will lead to a specialization of pathogen subpopulations, eventually leading to speciation. Thus host jumps and the successive radiation might be the driving force behind diversification of downy mildews and other pathogens. The different hypothetical steps in the process can be exemplified using several downy mildew lineages. For example, *Pseudoperonospora cubensis* currently seems to be in the process of active radiation. A host jump from Cannabaceae to Cucurbitaceae had taken place in evolutionary recent times and led to a radiation in the naïve Cucurbitaceae (Runge et al. 2011a; Runge and Thines 2012). However, enough time has already passed to lead to genetically distinct lineages within *Pseudoperonospora cubensis* s.l., and differences in virulence are known, which can probably be linked to a beginning evolutionary arms-race (Lebeda et al. 2013; Kitter et al. 2015). In the genus *Bremia* two major host jumps are apparent, once to Carduoideae and later to Asteroideae (Choi and Thines 2015); the host jump to Carduoideae has already led to some diversification; the host jump to

Asteroidae seems to be very recent and has not led to a significant degree of differentiation. In the genus *Hyaloperonospora* several host jumps to families other than Brassicaceae are known (Göker et al. 2009b), but as the host groups outside Brassicaceae have not been studied in detail, yet, it is unclear, if these have already led to speciation. The floricolous downy mildews of the genus *Peronospora* are another example of radiation and subsequent speciation (Thines and Kummer 2013; Voglmayr 2003), after an innovation has evolved (in this case the ability to restrict sporulation to the flowers of the hosts and probably to adapt to the special molecular physiological environment of floral tissues). It is conceivable that after a radiation and the subsequent onset of evolutionary arms races, many pathogen subpopulations would be removed from their host and not be able to survive in an evolutionary arms race. This will lead to an extinction of many pathogen lineages and only few will be able to develop into independent and successful species. As the speciation rate of the hosts can be expected to be much lower than the speciation rate of pathogens (Yoshida et al. 2013, 2014), the primary factor deciding on the diversity of pathogens will be their ability to persist and to jump to new hosts. Over time, an extinction process can be expected to remove further species that cannot form a stable association with their hosts in which their detrimental effects on the hosts would be small enough for not being a significant factor for host fitness. This will lead to only few pathogen lineages surviving from a specific host jump and radiation process. Thus, especially in older genera or groups within genera, it will be difficult or even impossible to determine the original host family from which the diversification of that group started. This is the situation currently found in the genera *Peronospora* and *Plasmopara*, in which the stem group is largely obscured by later host jumps (Göker et al. 2007; Riethmüller et al. 2002; Voglmayr 2003; Voglmayr et al. 2004). In conclusion, the hypothesis outlined means that host–pathogen associations will mostly not be stable over time, but pathogens will mostly need to retain the ability to jump hosts from time to time to establish a new radiation in order not to get extinct in the course of evolution.

With respect to the manipulation of hosts toward susceptibility, it remains vastly unknown, what constitutes the arsenal that eventually leads to successful colonization. Biotrophic pathogens have evolved toward stealth (Baxter et al. 2010), but the colonization of hosts is facilitated by the secretion of pathogenicity effectors, which interfere with the immune reaction of the hosts (Bozkurt et al. 2011; Thines and Kamoun 2010). Only few effectors will most likely be involved in the ability to jump hosts and to colonize a naïve group of hosts. Whether these belong to a core set of effectors, which are the core arsenal by which a certain group of pathogens is able to colonize hosts, or if these effectors would be additional, newly evolved ones, is not settled, yet. However, the finding from smut fungi that after a huge host jump gene loss rather than gene gain was observed (Sharma et al. 2014), seems to render it more likely that a modification of some core effector will lead to the ability to colonize new hosts, even though the alternative scenario cannot be excluded. In either case, the jump to a naïve host will most likely release a pathogen from specific R-protein–Avr-protein interaction (Solovyeva et al. 2015), which will open possibilities to rechannel resources during the evolutionary adaptation to the new hosts.

WHAT WE DON'T KNOW THAT WE DON'T KNOW

The things of which we do not know that we do not know them are the most important knowledge gaps. If it had been known that *Peronospora belbahrii* was not conspecific with *Peronospora lamii* from the beginning and had it been known that the disease could be distributed with seeds easily, it might have been possible to restrict the pathogen in a way that it would not have become a global issue. There are probably many factors in the epidemiology and evolution of *Peronospora* species we are currently not aware of and which

might lead to severe economic or ecological losses in the future. Research into various aspects of *Peronospora* diversity, ecology, evolution, molecular biology, and physiology will be necessary to fill knowledge gaps that will help to understand and manage *Peronospora* diseases better and to get prepared for future unpleasant surprises.

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