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Evolution of Disease Severity and Susceptibility in the Asteraceae to the Powdery Mildew *Golovinomyces latisporus*: Major Phylogenetic Structure Coupled With Highly Variable Disease Severity at Fine Scales

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Abstract

Pathogen host range and pathogen severity are dependent on interactions with their hosts and are hypothesized to have evolved as products of a coevolutionary arms race. An understanding of the factors that affect host range and pathogen severity is especially crucial in introduced pathogens that infect evolutionarily naïve hosts and cause substantial damage to ecosystems. Powdery mildews are detrimental pathogens found worldwide in managed and natural systems. *Golovinomyces latisporus* is a powdery mildew species that is especially damaging to plants within Asteraceae and to plants within the genus *Helianthus* in particular. In this study, we evaluated 126 species within Asteraceae to measure the role of host plant morphophysiological traits and evolutionary history on susceptibility to *G. latisporus* and disease severity. We observed phylogenetic signal in both susceptibility and severity within and among major clades of the Asteraceae. In general, there was a major phylogenetic structure of host severity to *G. latisporus*; however, there was some fine-scale phylogenetic variability. Phylogenetic statistical methods showed that chlorophyll content, biomass, stomatal index, and trichome density were not associated with disease severity, thus providing evidence that phylogenetic structure, rather than observed plant morphophysiological traits, is the most reliable predictor of pathogen severity. This work sheds light on the role that evolutionary history plays in plant susceptibility and severity to disease and underscores the relative unimportance of commonly assessed host plant traits in powdery mildew severity.

Keywords: evolution, *Helianthus*, morphophysiological traits, phylogeny, powdery mildew, susceptibility

The ability for a pathogen to cause disease and the amount of disease caused are dependent on a variety of host–pathogen interactions (Gilbert and Parker 2016). The biological and genetic factors associated with disease are hypothesized to have evolved as products of a coevolutionary arms race between pathogens and their hosts (Anderson et al. 2010). Plant pathogens are known to decrease the fitness of their hosts, resulting in evolutionary pressures on plants to evolve different modes of defense (Goss and Bergelson 2007). Plants defend themselves against pathogens through morphological adaptations as well as the production of constitutive and induced chemical defenses (Thaler et al. 1999; Zaynab et al. 2018). An understanding of the factors that affect host range and severity of pathogens is a crucial avenue of research. This is especially the case for introduced plant pathogens affecting novel plant hosts, given the extent to which these novel interactions are causing damage to ecosystems throughout the world (Ellison et al. 2005; Loo 2008; Mack 2000; Stajich et al. 2009).

Predicting the host range and severity of pathogens can be essential for limiting their impact and understanding their spread in a variety of ecological systems. Pathogen host range is often dictated by a suite of underlying morphological and chemical traits that can be described as phylogenetic signal (Gilbert and Webb 2007; Mason et al. 2016; Münkemüller et al. 2012). Research has reported that phylogenetic signal can be a valuable predictor of pathogen severity as well (Gilbert and Parker 2016; Gilbert et al. 2015). However, the phylogenetic patterns of host range and severity, as well as the traits associated with pathogen severity, remain relatively unknown.

There has been an increase in reports of the damage and spread of the common fungal pathogen powdery mildew in both agricultural and natural settings (Ale-Agha et al. 2000, 2004; Gent et al. 2013; Kiss 2005; Lipps and Madden 1989). Powdery mildews are obligate parasites (Braun and Cooke 2012) that can infect more than 10,000 angiosperm species worldwide (Amano 1986), including a number of vegetables, fruits, and ornamental plants (Westcott and Horst 1990). Powdery mildew first colonizes its hosts as white powdery spots that can spread over large areas of the plant and decrease its growth and its flower and fruit quantity (Daughtrey and Benson 2005). Favorable conditions for the growth of the disease include mild weather with temperatures of approximately 25°C (Gubler et al. 1999). High humidity can be favorable for infection and conidial (asexual spores) survival; however, dry conditions are favorable for colonization, sporulation, and dispersal (McGrath 2017). Control costs exceed hundreds of millions of dollars annually in California alone (Sambucci et al. 2014).

Golovinomyces latisporus is a powdery mildew species that is especially damaging to plants within Asteraceae and to plants within the genus *Helianthus* in particular (Braun and Cook 2012; Kontaxis 1986; Qiu et al. 2020). The Asteraceae is the largest family of flowering plants, with more than 418 genera and 2,413 described species. Plants within Asteraceae are highly morphologically and physiologically diverse (Funk et al. 2009). The genus *Helianthus* (sunflowers) contains approximately 52 species of annual or perennial plants native throughout North America, with several species cultivated or naturalized in locations worldwide (Heiser et al. 1969; Schilling 2006). *Helianthus* species are grown ornamentally as well as agriculturally for their oil and seeds. The genus is also a strong model system for studies in evolutionary ecology and, specifically, the evolution of host defense, since its species contain a broad range of morphology, physiology, and secondary chemistry (Mason and Donovan 2015; Mason et al. 2016).

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The objectives of this research were to test whether the success of *G. latisporus* to multiple genera within Asteraceae is a function of (i) the morphophysiological traits of the host plant and/or (ii) the evolutionary relatedness of the host plants. In particular, we evaluated whether host evolutionary history is a predictor for powdery mildew host range and severity within the Asteraceae.

Materials and Methods

We conducted two separate greenhouse experiments. In the first experiment, we evaluated the susceptibility of 126 host plant species within Asteraceae to *G. latisporus*. In the second, we evaluated the severity of 62 susceptible Asteraceae species, listed in Supplementary Table S1, to *G. latisporus*.

Host range experiment. The 126 species chosen were based on wild collected seeds available from the U.S. National Plant Germplasm System in 2019. Seeds were planted at the Douglas Research Conservatory (University of Washington, Seattle, WA) per the recommendations supplied by the U.S. National Plant Germplasm System in 2019. After germination, seedlings were potted in Sunshine 4 potting soil (SunGro, Bellevue, WA) in 8.9 × 8.9-cm pots. Each pot contained one species of plant. The number of seedlings grown per species ranged from 5 to 50, depending on germination success.

Plants were inoculated with a powdery mildew specimen growing on *H. annuus* at the University of Washington Farm (Seattle, WA). Prior to the experiment, the powdery mildew used for inoculum in this study underwent multilocus phylogenetic and morphological evaluations and was identified as *G. latisporus* (U. Braun) P.L. Qiu & S.Y. Liu (see specimen HMJAU-PM91853 in Supplementary Fig. S3 from Qiu et al. 2020).

The inoculum was made by cutting infected leaves into small pieces using a sterile blade. The leaf pieces were placed into a sterile 50-ml Falcon tube with 10 ml of 0.001% Tween 20 and vortexed for 30 s. Spores were counted using a hemocytometer and the concentrations were adjusted to 10,000 spores/ml. Inoculations were applied onto the plant using a hand sprayer until the inoculum was visibly running off the leaf. Seedlings were grown for 1 month and the inoculum was applied once every 3 days. Signs of powdery mildew were evaluated every 3 days prior to inoculum applications. The plants were watered and fertilized on an as-needed basis using a subirrigation system to control for the effect of overhead watering on powdery mildew growth. To minimize insect damage, a soil injection of imidacloprid (Xytect 2F) was applied to all of the seedlings. If powdery mildew colonies were observed from naked-eye assessments on any of the seedlings grown, the species was considered a susceptible host to *G. latisporus*.

Severity experiment. Sixty-two of the species that were susceptible to *G. latisporus* in the host range experiment (Supplementary Table S1) were consequently evaluated for their severity to *G. latisporus.* Three seedlings from each species were planted in 8.9-cm pots (one seedling per pot). The inoculum was prepared as described above. Unlike the host range experiment in which the inoculum was applied every 3 days, the inoculum was applied only once in the severity experiment at the onset of the experiment. Experiments were conducted in a randomized block design. The average temperature in the greenhouse during the experiment was 22.7°C, and the average relative humidity was 64.0%. The plants were watered and fertilized on an as-needed basis using a subirrigation system to control for the effect of overhead watering on powdery mildew growth. To minimize insect damage, a soil injection of imidacloprid (Xytect 2F) was applied to all of the seedlings.

Disease severity measurements were taken once a week for 2 months using naked-eye assessments to estimate the percentage of the surface area of the plant colonized by powdery mildew (the stem and both the abaxial and adaxial sides of the leaves were included as total surface area). Naked eye assessments estimating disease severity based on disease coverage are common in powdery mildew studies (Grove and Bennett 2000; Moparthi and Bradshaw 2020) and were found to be as accurate as disease analysis software (Bade and Carmona 2011; Olmstead et al. 2001). Additionally, naked eye assessments are faster and more efficient than using disease analysis software, and they permit the inclusion of stem symptoms normally excluded from leaf image-based software approaches.

We also measured plant traits as a potential predictor of severity to *G. latisporus*. These traits were relative chlorophyll content, above- and belowground biomass, trichome density, stomata density, epidermal cell density, and stomatal index. Data for life history (perennial versus annual), host ploidy, and venation pattern were acquired from Kallamadi and Mulpuri (2016), Mason and Donovan (2015), and Qiu et al. (2019).

Relative chlorophyll content was measured in arbitrary units referred to as SPAD units using a Konica Minolta SPAD 502 Meter (Konica Minolta, Ramsey, NJ). The measurements are a suitable proxy for leaf nitrogen content (Uchino et al. 2013). Three measurements were taken per leaf on different aged leaves (first node, second node, and third node) on the last sampling day and then averaged to obtain a single SPAD unit value.

Above- and belowground biomass measurements were taken at the end of the experiment to determine the growth rate of the different plant species over the 2-month duration of the experiment. The plants were first placed in buckets full of water to wash soil from roots. They were then placed into brown paper bags and placed in a herbarium dryer for 4 days at 37.8°C. Above- and belowground biomass was separated and individually weighed using an OHAUS BW15US scale (OHAUS, Parsippany, NJ). The shoot-to-root ratio was calculated as the dry weight for belowground matter divided by the dry weight for aboveground matter.

After measuring biomass, trichome and stomata counts were acquired by taking pictures of leaf peels made on dry leaves with a compound microscope. Because plant traits are fairly conserved within species, one leaf was randomly selected from the center node of each plant (total of three leaves per species). Leaf peels were made by placing a thin layer of nail polish on the abaxial and adaxial leaf surface. The nail polish was removed from the leaf and placed onto a microscope slide. Pictures of the slides were taken using a compound microscope with an Olympus SC50 camera attached (Olympus Corporation, Tokyo, Japan). Trichome, stomata, and epidermal counts were calculated twice per leaf on the upper and lower portion of selected leaves (Fig. 1) using Olympus cellSens Imaging software. The two measurements were averaged together to calculate a mean measurement per leaf. The stomatal index was calculated according to the following:

$$\text{Stomatal index} = \text{Stomata per mm}^2 \times 100 / \left(\text{epidermal cells per mm}^2 + \text{stomata per mm}^2\right)$$

Phylogenetic inference. We generated a species-level phylogeny of 186 species (Supplementary File S1) using a Python implementation (PyPHLAWD; Smith and Walker 2019) of the PHLAWD pipeline (Smith and Brown 2018). Briefly, we used PHLAWD to gather sequence data from NCBI and to construct putative orthologs, perform quality filtering (i.e., eliminate sequences <300 bp in length and clusters with five represented taxa or less), and concatenate the resulting sequences. We fit a maximum likelihood tree with 100 bootstraps using RAxML using a backbone constraint tree (Supplementary File S2) based on Mandel et al. (2019), Urbatsch et al. (2000), and the Angiosperm Phylogeny Group (2016). Some fine-scale placements of taxa within the genus *Helianthus* differ from the most well-resolved phylogeny of the diploid backbone of the genus, almost certainly attributable to the inclusion of polyploid species and the known hybrid origins of some such taxa and thus reticulate evolution within genus *Helianthus*. Lack of monophyly for some taxa should be interpreted with this caveat in mind (Stephens et al. 2015; Timme et al. 2007).

Statistical analyses. Area under the disease progress curve (AUDPC) values were calculated for the disease severity data using the formula recommended by Sparks et al. (2008). The AUDPC is a useful tool for comparing disease intensity over time (Sparks et al. 2008) and is commonly used in controlled environment studies

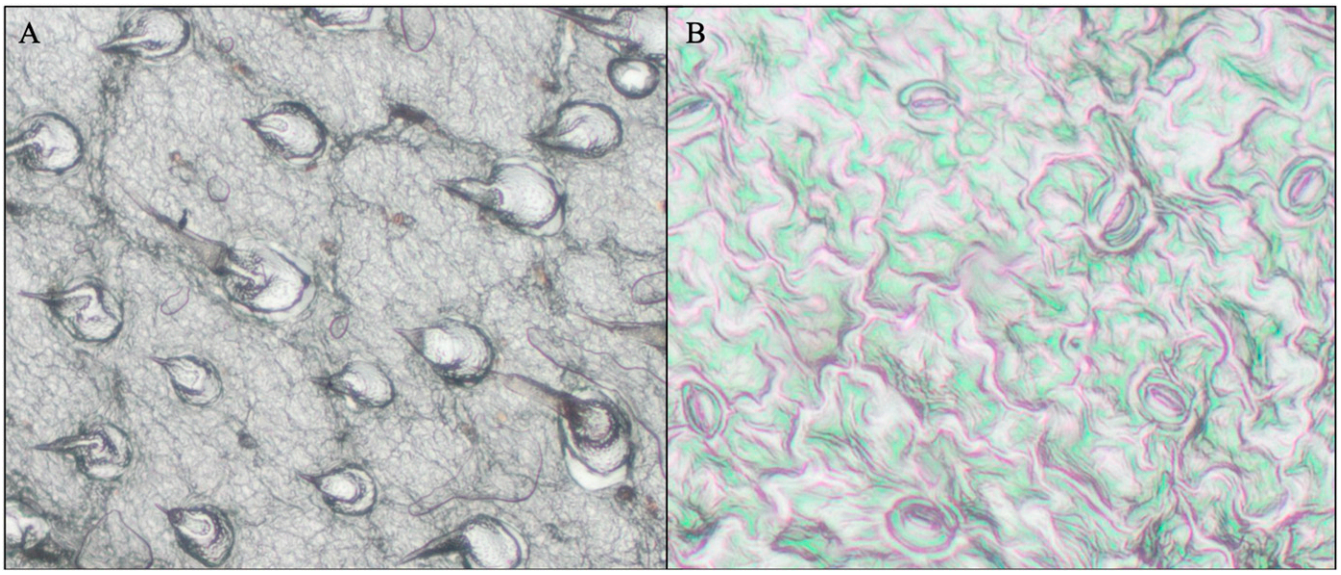

Fig. 1. A, The abaxial leaf surface of *Helianthus* trichomes. **B,** The adaxial leaf surface of *Helianthus* epidermal and stomata cells.

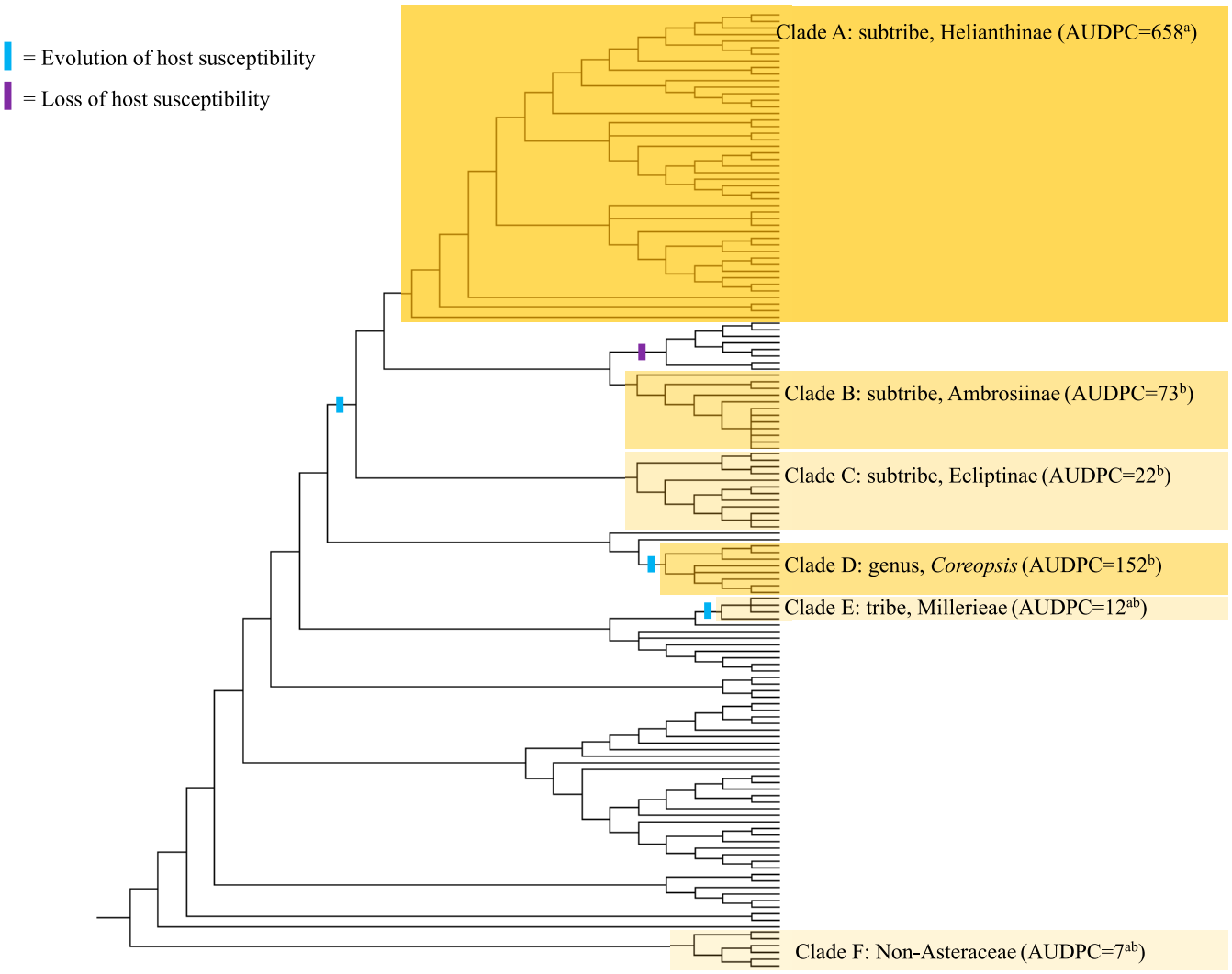

Fig. 2. A phylogenetic tree of the Asteraceae with major evolutionary events added using a parsimony approach. The average disease severity of the species within the highlighted clades to *Golovinomyces latisporus* is presented as an area under the disease progress curve (AUDPC) value. Darker shades of yellow highlighting the major clades signify higher severity values. Taxa within clade A (composed of mainly *Helianthus* spp.) exhibited the highest disease severity. Clades with the same letters are not statistically different by conventional analysis of variance ($P < 0.05$). Evolutionary events of taxa not in the Asteraceae were not included.

(Cséplö et al. 2013; Li 2018; McCaghey et al. 2017; Moparthi and Bradshaw 2020). This type of curve is best suited when evaluating disease severity because it generates a single numeric value that accounts for disease progress over time. AUDPC data were transformed using a square root transformation to satisfy the assumptions of normality and analyzed in an analysis of variance (ANOVA) to measure the effect of phylogenetic clade on severity to *G. latisporus*. Host plant species were grouped based on their clades presented in Figures 2 and 3. Post hoc tests were based on Tukey's honest significant difference (HSD; $\alpha = 0.05$). All analyses were performed using R software (version 3.31; R Core Team 2017).

To determine the effect of plant traits on disease severity, phylogenetic ANOVA (Garland et al. 1993) was used to compare the results from conventional ANOVA analyses. Both approaches were used to determine the effects of life history, ploidy, and venation pattern on disease severity (calculated as AUDPC value). In the conventional ANOVA, differences between treatment means were based on Tukey's HSD ($\alpha = 0.05$). For the phylogenetic ANOVA, the Phytools package (Revell 2012) was used, and differences between treatment means were based on the Holm-Bonferroni method ($\alpha = 0.05$).

Generalized linear regression was used to analyze the effect of total biomass, aboveground biomass, belowground biomass, shoot-to-root ratio, relative chlorophyll density, trichome density, and stomatal index on disease severity (calculated as AUDPC value). The traits were evaluated individually and in a model that accounted for interaction effects. Multicollinear predictor variables were not used in the same model. For example, total biomass, shoot-to-root ratio, and belowground and aboveground biomass were not used in the same model. For phylogenetic comparative analyses, we extended zero-length terminal branches (an occasional outcome of phylogenetic inference routines) by the median of all nonzero terminal branch lengths on the tree. We also substituted *Zinnia flavicoma*, which was represented on the tree but not in our phenotypic data, with a closely related species (*Z. elegans*), which was represented in our phenotypic data but not on the original tree. We performed phylogenetic generalized least squares regression using the *phylolm* package (Ho and Ané 2014) to assess the relationship between disease severity (AUDPC) and growth rate, shoot-to-root ratio, chlorophyll content, trichome density, and stomatal index.

Results

Host range experiment. Signs of powdery mildew were first noted 6 days postinoculation. Of the 126 species tested, 57 were not susceptible to *G. latisporus* and 69 were susceptible to *G. latisporus* to some extent (as defined by visual assessments of colonies forming on the leaves). The susceptibility of all species as hosts is denoted in Supplementary Table S1. The species that were experimentally observed to be hosts of *G. latisporus*, including those that were previously reported to be hosts, are shown in Figures 3, 4, and 5. It is possible, yet unlikely, that contaminating spores from other species of powdery mildew inoculated the host species evaluated.

Severity experiment. All of the *Helianthus* species were susceptible to *G. latisporus* (Fig. 3) and, overall, species within *Helianthus* exhibited the most severe *G. latisporus* infections compared with the other genera evaluated (Fig. 6). However, severity within the genus *Helianthus* ranged from the most severe in *H. carnosus*, which is an endangered species (AUDPC = 2,308, SD = 530.46; U.S. Department of Agriculture 2020) to the least severe in *H. decapetalus* (AUDPC = 4.67, SD = 5.35). Overall, there was considerable variation in severity among the susceptible host plants tested (Fig. 6).

Phylogenetic inference. A species-level phylogenetic tree consisting of 186 predominately Asteraceae taxa was generated for this study (Fig. 2). The tree consisted of taxa that were evaluated in this study or taxa that were previously listed as susceptible hosts for *G. latisporus.* The most parsimonious explanation is that host susceptibility (defined as the ability to show noticeable powdery mildew infections) within Asteraceae evolved separately at least five times and was lost at least four times (Figs. 2, 3, 4, and 5). However, whether host susceptibility to *G. latisporus* evolved in multiple separate events outside of the Asteraceae cannot be deduced from the current study, as only one genus outside of Asteraceae (*Abelmoschus*) was a susceptible host.

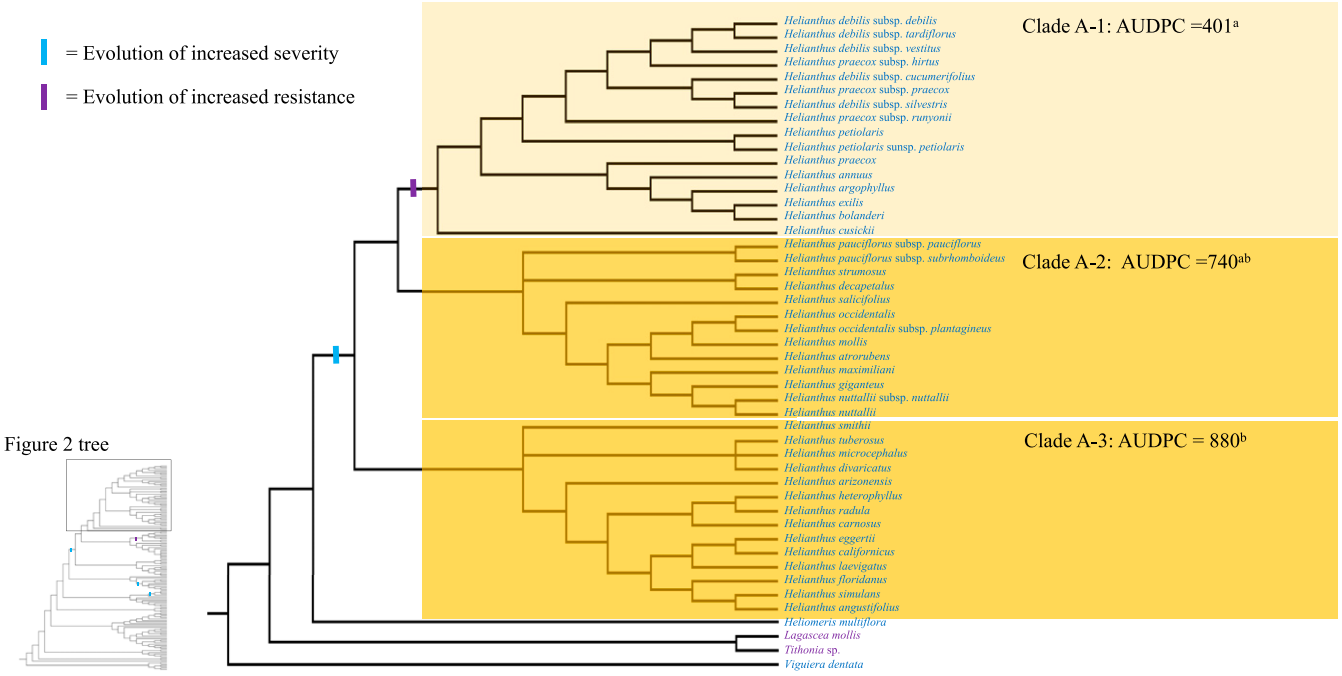

Fig. 3. A portion of the phylogenetic tree presented in Figure 2. Evolutionary events were added using a parsimony approach. Taxa in blue were experimentally determined in this study to be hosts of *Golovinomyces latisporus*, taxa in purple were previously reported as hosts, and taxa in black were experimentally determined in this study to not be a susceptible host. Darker shades of yellow highlighting the major clades signify higher disease severity values. The average severity of the species within the highlighted clades to *G. latisporus* is presented as an area under the disease progress curve (AUDPC) value. Clades with different letters are nearly significantly different using conventional analysis of variance and Tukey's honest significant difference ($P = 0.06$). Clade A-1, which primarily consists of annual species, is less susceptible to disease than clade A-3, which primarily consists of perennial species.

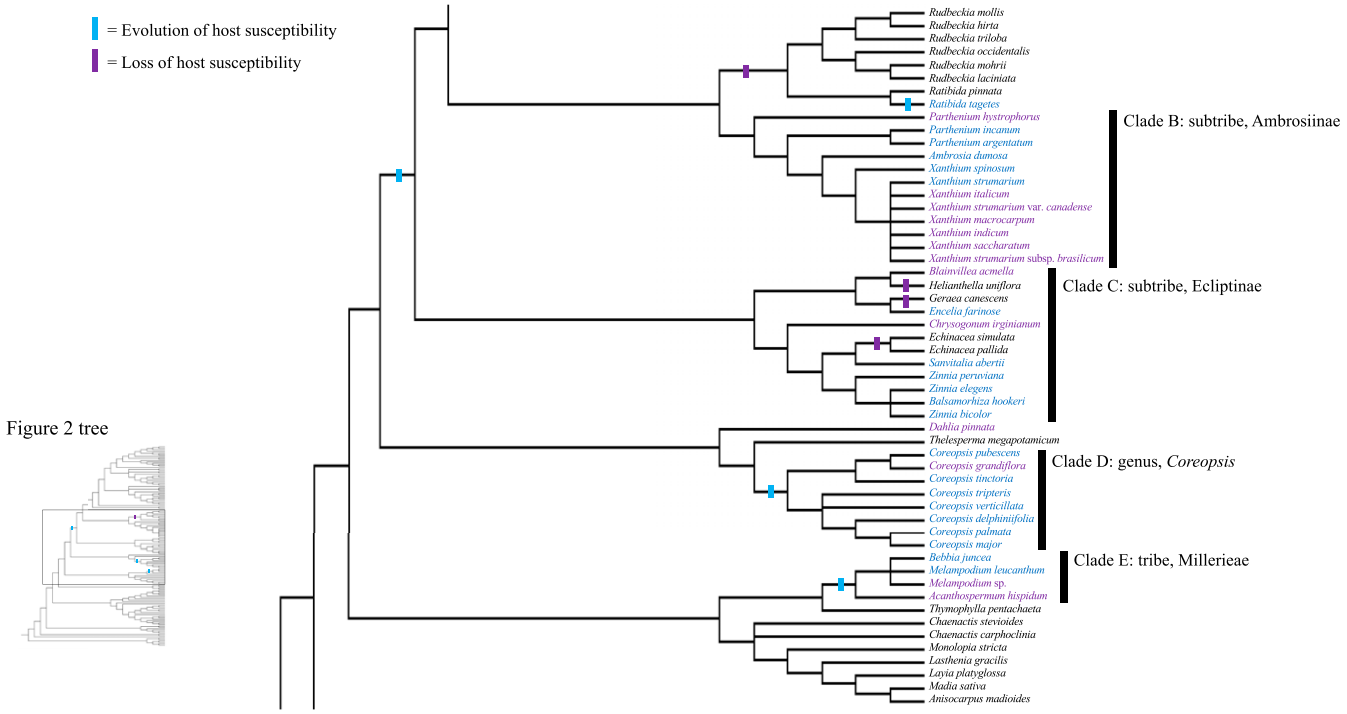

Fig. 4. A portion of the phylogenetic tree presented in Figure 2. Evolutionary events were added based on a parsimony approach. Taxa in blue were experimentally determined to be susceptible to *Golovinomyces latisporus* in this study, while taxa in purple were previously reported to be susceptible. Host susceptibility was gained and lost throughout the Asteraceae. *Dhalia pinnata* was shown in 2020 to be a host of *G. ambrosiae*, not *G. latisporus*, which was reported in the past (Qiu et al. 2020).

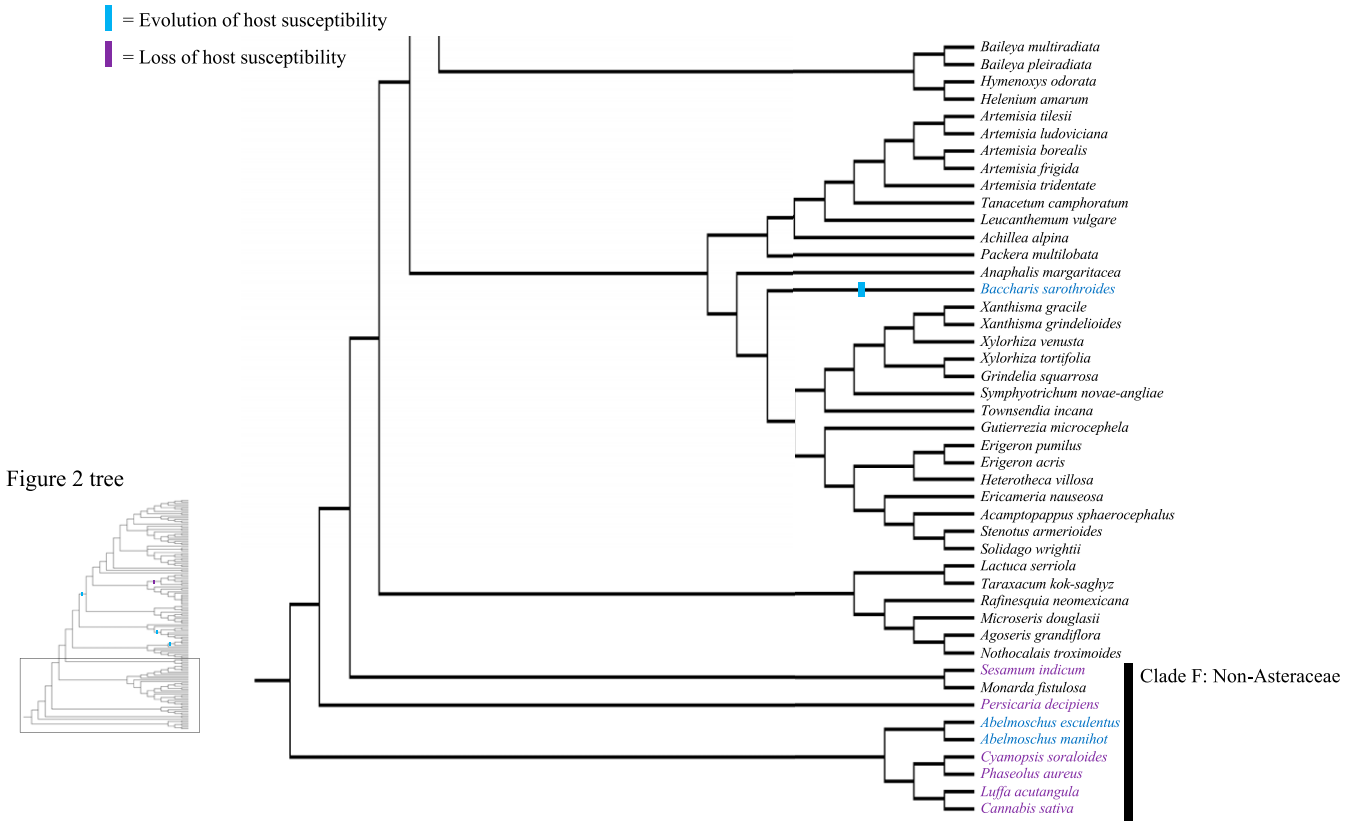

Fig. 5. A portion of the phylogenetic tree presented in Figure 2. Evolutionary events were added based on a parsimony approach. Taxa in blue were experimentally determined to be susceptible to *Golovinomyces latisporus* in this study, taxa in purple were previously reported to be susceptible, and taxa in black were experimentally determined in this study to not be a susceptible host. Evolutionary events among taxa not in the Asteraceae were not included.

Phylogenetic clades within Asteraceae and also within genus *Helianthus* differed statistically in their disease severity to *G. latisporus*. There were five large monophyletic clades within the Asteraceae in which all of the taxa were susceptible to *G. latisporus* (Fig. 2). The average disease severity of the taxa within the five clades differed significantly from each other. Clade A, which consisted of species within the Helianthinae, had significantly higher disease severity than clades B, C, and D (all $P < 0.05$; Fig. 2). Within the *Helianthus* clade, there were three separate monophyletic subclades (Fig. 3). Subclade A-1 consisted of predominantly annual species, whereas subclades A-2 and A-3 consisted of predominantly perennial species. The three major subclades within the *Helianthus* clade were nearly significantly different, as clade A-3 tended to have higher disease severity than clade A-1 ($P = 0.06$; Fig. 3). Additionally, there were areas of the phylogeny where there was a substantial amount of variation within extremely closely related species (where sister species and sometimes subspecies had divergent susceptibility). For example, in the clade that consisted of *H. microcephalus*, *H. smithii*, and *H. tuberosus*, both *H. microcephalus* and *H. tuberosus* had high disease severity compared with *H. smithii.*

Trait evaluations. There were no statistically significant differences in disease severity among life history, ploidy levels, venation patterns, or native locality in a phylogenetic ANOVA analyses. However, in a conventional ANOVA, life history, venation pattern, and native locality were significant predictors of disease severity (Table 1). Specifically, annual species and species with a longitudinal leaf venation pattern had significantly less severe disease infections. Because conventional and phylogenetic ANOVA differed in their results, it cannot be ascertained whether the observed disease severity was associated with these traits. There was not a sufficient number of evolutionarily independent origins in life history, venation, or native locality to be confident of the role of these traits in disease severity. For example, the perennial clades of genus *Helianthus* had high disease severity relative to the annual clade; however, there have only been approximately three transitions between annual and perennial life history as sunflowers have diversified. Thus, this limits the ability to conclude that increased severity is attributable to life history. Additionally, some of the traits could be associated with disease severity; however, the low sample size (i.e., $n = 2$ and 5 for tetraploidy and hexaploidy, respectively) prohibited the use of inferential statistics, even with large differences in the disease severity means based on ploidy.

There was no significant effect of chlorophyll content, stomatal index, trichome density, growth rate, or shoot-to-root ratio on disease severity in a phylogenetic least squares regression analysis (all $P > 0.05$) and after accounting for multiple tests (Holm 1979). In a generalized linear regression, which does not account for phylogenetic relatedness, none of the plant traits were significant predictors of disease severity.

Discussion

Evolutionary history was a reliable predictor of susceptibility and severity of *G. latisporus* to species within Asteraceae. Five clades within Asteraceae were susceptible to *G. latisporus* (Fig. 2). Within

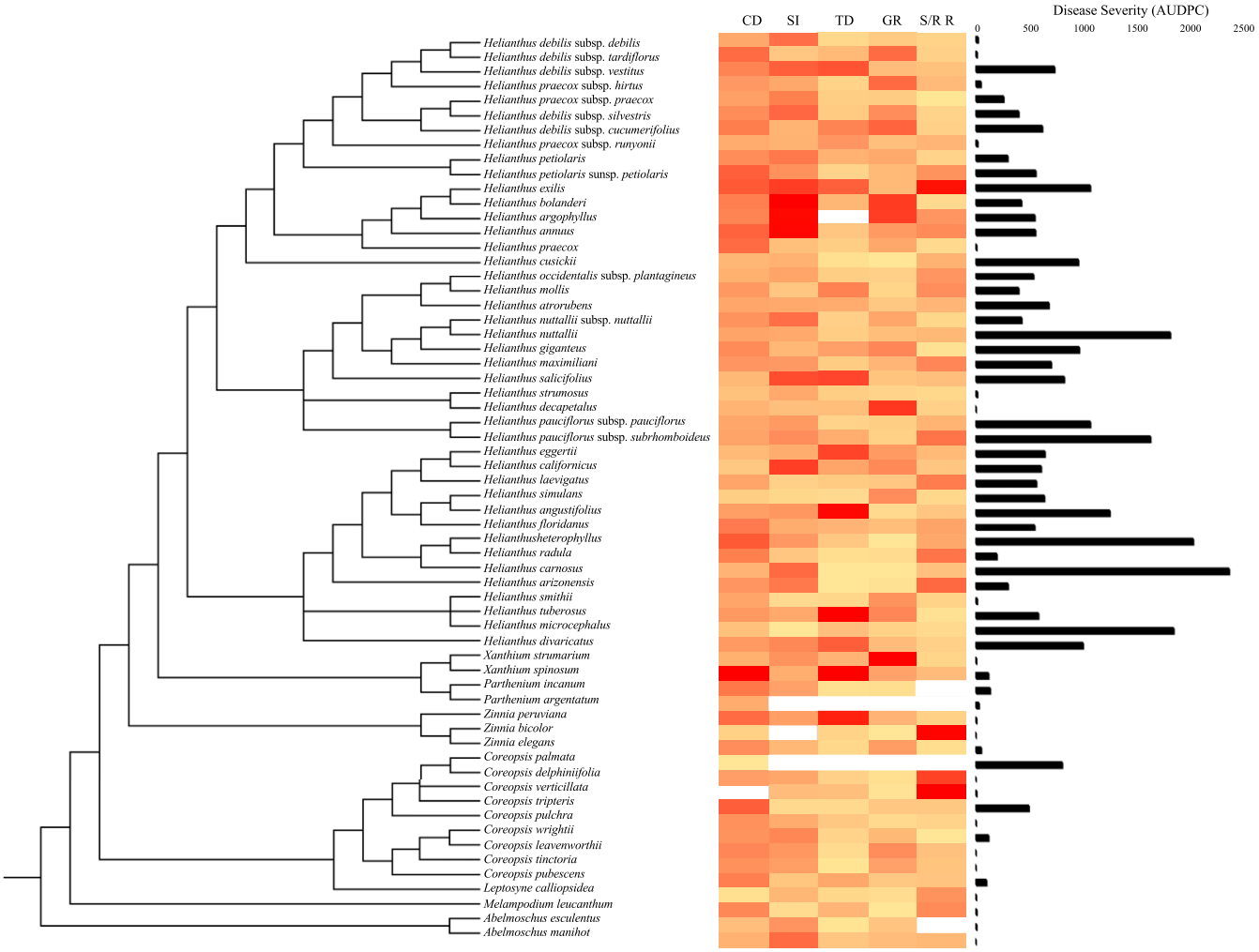

Fig. 6. Phylogeny of the taxa that were evaluated for their severity to *Golovinomyces latisporus* in this study. The disease severity of the different taxa is shown in a bar graph to the right. Severity is presented as an area under the disease progress curve (AUDPC) value. A heat map is shown of the average value for each of the different traits measured in this study. CD = chlorophyll density, SI = stomatal index, TD = trichome density, GR = growth rate, and S/R = shoot-to-root ratio.

Table 1. Results of conventional and phylogenetic analysis of variance (ANOVA) evaluating the effects of plant host traits on disease severity

Plant trait	AUDPC mean[z]
Growth form	
Annual	475.8[a1]
Perennial	832.67[a2]
Ploidy	
Diploid (2n)	804.44[a1]
Tetraploid (4n)	284.833[a1]
Hexaploid (6n)	743.08[a1]
Venation pattern	
Intermediate/variable	1,040.28[a34]
Longitudinal	2,144.37[a4]
Palmate	350.73[a2]
Pinnate	463.46[a23]

[z] Means with the same number within trait groupings are not statistically different ($P < 0.05$) in an ANOVA. Means with the same letter within trait groupings are not significantly different ($P < 0.05$) in a phylogenetic ANOVA. AUDPC = area under the disease progress curve.

the Asteraceae, the phylogenetic structure of severity was seen not only at the family level but also at the genus level. For example, taxa within clade A (Fig. 2) had the highest disease severity measurements. Additionally, within clade A, clade A-3 had the most severe infections (Fig. 3). The phylogenetic clumping of hosts reported in this study agrees with previous work that reported that evolutionary relationships between hosts can be a valid predictor of host range and severity to fungal pathogens as well as insect herbivores (De Vienne et al. 2009; Gilbert and Parker 2016; Gilbert and Webb 2007; Gilbert et al. 2015; King and Cable 2007; Mech et al. 2019; Moore and Gotelli 1996; Perlman and Jaenike 2003).

This study is the first confirmed report of susceptibility to *G. latisporus* for 58 of the examined Asteraceae hosts (Farr and Rossman 2020). However, many of these hosts are within Heliantheae, which is listed as a host in Braun and Cook (2012). Qiu et al. (2020) reported that *Rudbeckia* species, based on morphological assessments, were listed as a likely host of *G. latisporus*. In the host range evaluations performed in the current study, *Rudbeckia* species were unable to be inoculated with *G. latisporus*. It is possible that the genus *Rudbeckia* is a host for *G. latisporus* but not for the specific strain we evaluated (the inclusion of *Rudbeckia* spp. in the host range of the *G. latisporus* was mainly based on morphological analyses, including the particular conidial germination pattern [of European collections], according to U. Braun, *personal communication*). Identifying *G. latisporus* based solely on morphological traits can be very difficult, and this study highlights the need for a multilocus genetic approach on *Rudbeckia* spp. infected with powdery mildew. In general, it has to be taken into consideration that host range experiments are sometimes influenced by the provenience of the inoculum. Blumer (1967) discussed previously performed host range experiments (Blumer 1952; Hammarlund 1945; Schmitt 1955) and pointed to inconsistencies and sometimes even conflicting results in cases of experiments with powdery mildews of different origins, such as different continents.

The role that constitutive morphophysiological plant traits play in defense against powdery mildew, and whether plant morphology and physiology predicts disease, is not known and past studies in this area have been limited and contradictory (e.g., Chattopadhyay et al. 2011; Jarosz et al. 1982; Kloos et al. 2005). Consistent with these past contradictions, in this study, a conventional ANOVA revealed significant differences in the disease severity on hosts based on their life history and leaf venation patterns. However, there was no significant relationship between any of the plant traits tested and disease severity when using phylogenetic ANOVA, which accounts for phylogenetic history and the evolution of shared traits through a common ancestor. Nonetheless, the evaluation of additional traits may yield different results. For example, by pooling data from multiple studies, Mason et al. (2016) found that resistance to powdery mildew was strongly predicted by the abundance of secondary metabolites and that most morphophysiological trait measurements, at the leaf level, were not correlated with powdery mildew resistance.

To our knowledge, this is the first study to observe a phylogenetic structure to disease severity at both the family and genus levels within the same plant-pathogen system. The data presented provide evidence that host phylogeny is a critical predictor of disease severity and susceptibility to pathogens. Future work should evaluate clades of other lineages that vary in morphological, physiological, and chemical traits and susceptibility to determine whether other systems exhibit similar patterns of susceptibility and severity. Additionally, the genomes of closely related species that differ in susceptibility should be compared and mined for genetic differences that could be related to defense.

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