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A survey of highly influential studies on plant pathogen effectors during the last two decades (2000-2020)

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Abstract

Plant effector biology is a research area that describes how plant-associated organisms modulate host structures and functions to promote colonization by using small molecules (effectors). In this article, we analyzed the 249 most highly-cited publications focused on plant pathogen effectors (aka Highly Influential studies on plant Pathogen Effectors; thereafter HIPEs) published between 2000 and 2020. This analysis identified outstanding countries, organizations, and journals that contributed HIPEs, as well as the evolution of research trends, model molecules, and model organisms over the last two decades. We notably show an increasing proportion of studies focused on effectors of biotrophic and hemibiotrophic fungi upon time. Our snapshot of the top tier plant effector biology papers will help readers gain a comprehensive and analytical understanding of this research area.

Keywords

Bibliometric pipeline, Web of Science, plant immunity, avirulence, virulence, pathogenicity, receptor

Introduction

Plant pathogens threaten agricultural production by triggering dramatic yield losses worldwide (Savary *et al.*, 2019). The effector biology research field explains how pathogens manipulate their host(s) to promote infection through the modulation of host structures and processes, and aims at leveraging that knowledge to ultimately improve plant health (Win *et al.*, 2012). Since the 2000s, this field of research grew spectacularly, with an exponential increase in the number of publications ([https://www.webofscience.com/Supplementary Figure S1](https://www.webofscience.com/Supplementary_Figure_S1)). During these two decades, our understanding of effector diversity and functions has improved, notably thanks to functional genomic studies. However, there are only a few studies that comprehensively inventory the major findings and concepts of plant effector biology, which makes it difficult for junior researchers to gain a broad expert and conceptual understanding of the research field.

To build a snapshot of top tier research in plant effector biology, we implemented the 'HIP in' ('Highly-Influential Publication in' ...) method that we recently described (Petre *et al.*, 2021). We report here a bibliometric analysis of 249

Highly Influential (*i.e.* highly cited) papers on plant Pathogen Effectors (thereafter HIPEs) published between 2000 and 2020. We describe the concepts, model objects, and findings shared by HIPEs, as well as the research community that shared them. We notably show the increasing importance of fungi as model pathogens over time, and highlight key fungal species.

A bibliometric pipeline identifies 249 highly influential publications addressing plant pathogen effectors

To identify the most influential publications that addressed plant pathogen effectors over the last two decades, we implemented a previously-described bibliometric pipeline (Petre *et al.*, 2021), which mostly uses the Web of Science database (<https://www.webofscience.com>) and a reference management software (here Mendeley). We selected the top three most cited research articles or reviews for each year between 2000 and 2020, which we identified via three successive searches using the key words 'plant pathogen effectors', 'plant pathogen avirulent effectors', and 'plant pathogen virulent

effectors' ([Figure 1A](#); [Dataset 1](#); see [Supplementary Methods](#) and [Supplementary Figure S2](#) for details). In total, we collected and archived 249 HIPEs (127 research articles and 122 reviews; hereafter the 'HIPE collection') on the following public web address: https://www.zotero.org/groups/4410902/hipe_collection/library.

The HIPEs represents 4% of all the publications identified *via* the three searches above mentioned, but their annual citation rate is approximately four times higher (25 *vs.* 6 on average; [Figure 1B](#)). The HIPE with the highest number of citations (6503) and annual citation rate (414) is the review that presented the

seminal zig-zag model (Jones and Dangl, 2006). Interestingly, the current five years impact factors of the journals in which HIPEs were published do not correlate with HIPEs annual citation rate, indicating that the journal impact factor is a poor indicator of HIPEs influence ([Figure 1C](#)). As a note, only 19 out of 249 HIPEs overlap with the collection of highly-cited papers in plant immunity (HIPPYs) described in our previous paper (Petre *et al.*, 2021; [Dataset 1, column B](#)). To summarize, HIPEs represent an original collection of influential studies that pertains to plant pathogen effectors, and that is suitable for further analyses.

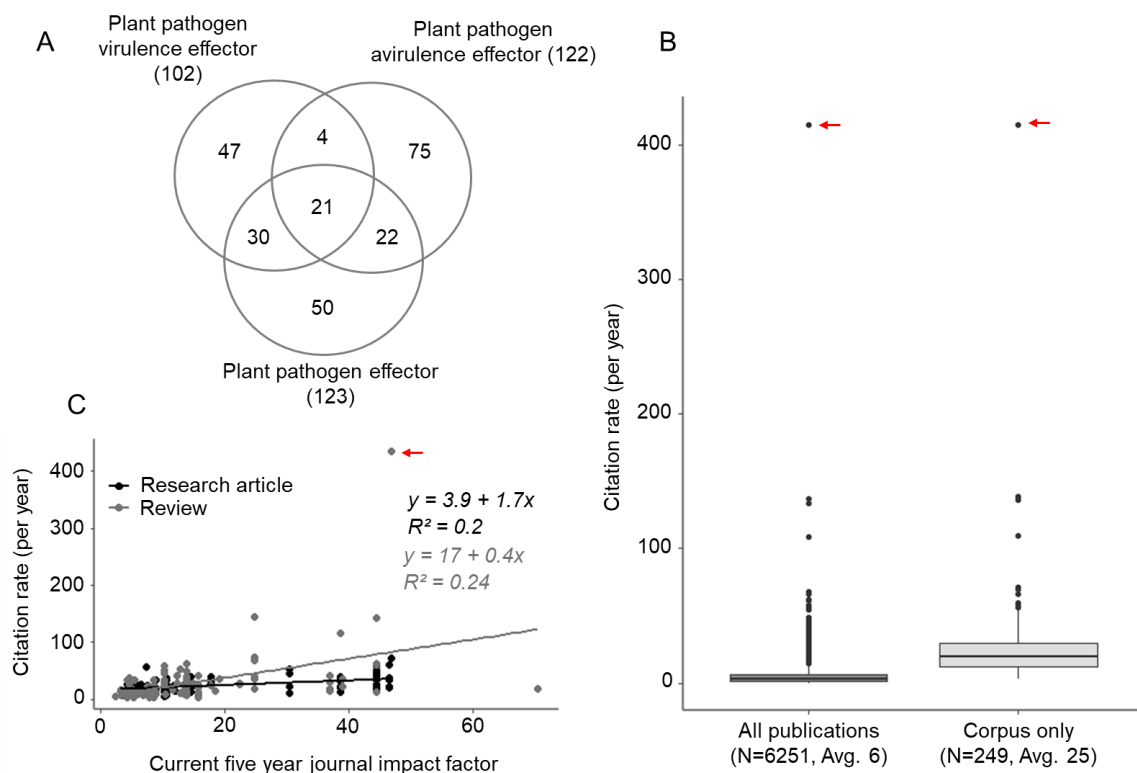


Figure 1. HIPEs are highly cited studies addressing plant pathogen effectors

(A) Venn diagram indicating the number of overlapping publications between the three group of key words ('plant pathogen effectors', 'plant pathogen avirulence effectors' and 'plant pathogen virulence effectors') used to build the HIPE collection. The number of publications is shown between parentheses. (B) Boxplots displaying the annual citation rate of all publications identified with the keyword searches (left-hand side; 'All publications') and the HIPEs only (right-hand side; 'Corpus only'). The boxplot outliers are indicated as dots. The number and the average of publications considered is indicated below each boxplot (N and Avg value, respectively). (C) Scatterplot displaying the annual citation rate of individual HIPEs according to the value of the current five-year journal impact factor of the journal in which the HIPEs were published. Black and grey dots indicate research articles and reviews, respectively. Linear trendlines are indicated for each article type along with trendline equations and r-squared values, with the same color-code as previously. In (B) and (C), the red arrow indicates the HIPE with the highest annual citation rate, which corresponds to the 2006 review by Jones and Dangl that presented the zig-zag model of the plant immune system. The raw data used to build this figure are available in the [Dataset 1](#).

A small influential community publishes the majority of the HIPEs

To identify the research community that publishes the HIPEs, we extracted from HIPEs metadata the main countries and institutions to which HIPEs corresponding authors are affiliated, as well as the journals that published them. Overall, 19 countries, 87 institutions (comprising 154 affiliated corresponding authors), and 67 journals published the HIPEs ([Dataset 1](#)). Interestingly, only a handful of scientific actors contributed most of the collection ([Table 1](#)). Indeed, three countries (USA, UK, and Germany) published 62% of the

HIPEs, whereas four institutions published a quarter of the HIPEs: the Max Planck Institute (MPI, Germany), The Sainsbury Laboratory (TSL, UK), the National Research Institute for Agriculture, Food, and Environment (INRAE, France) and the Wageningen University & Research (WUR, Netherlands). Also, four journals (Science, Annual Review of Phytopathology, PNAS, and The Plant Cell) contributed over a quarter of the HIPEs. Altogether, this analysis indicates that HIPEs are shared by a restricted number of academic actors mostly based in Western Europe and in the USA.

Table 1. Top countries, institutions, and journals that publish the most HIPEs.

Country, institution, or journal ^a	Number of HIPEs	Number of citations	Number of corresponding authors	Current 5-year journal impact factor
USA	88	25,167	52	-
UK	35	13,939	25	-
Germany	31	7,581	19	-
INRAE (France)	18	3,099	13	-
TSL (UK)	15	10,082	7	-
MPI (Germany)	15	4,034	10	-
WUR (Netherlands)	14	3,190	6	-
Science	20	7,013	-	44.37
Annual Review of Phytopathology	19	4,925	-	13.87
PNAS	17	4,702	-	10.62
The Plant Cell	17	3,686	-	10.14

^a USA: United States of America; UK: United Kingdom; INRAE: Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement; TSL: The Sainsbury Laboratory; MPI: Max Planck Institute; WUR: Wageningen University & Research; PNAS: Proceedings of the National Academy of Science of the USA.

HIPEs collectively address seven main research questions, whose relative importance within the HIPE collection evolved over time

To identify the main research questions addressed by the HIPEs, we performed an iterative analytical reading combined with key word tagging of all the collection aimed at identifying HIPEs main research topics and sub-topics. This analysis identified seven main research topics as follow: 1) the 'PTI' (PAMP-triggered immunity; *what is the interplay between PTI and effectors?*; 10 HIPEs), 2) the 'ETI' (Effector-triggered immunity; *what is the interplay between ETI and effectors?*; 41 HIPEs), 3) the 'ETS' (Effector-triggered susceptibility; *how do effectors modulate host functions?*; 78 HIPEs), 4) the 'Effector

trafficking' topic (*how do pathogens deliver effectors to the host?*; 16 HIPEs), 5) the 'Pathogen highlight' topic (*what is the current knowledge in the field for specific pathogen species?*; 12 HIPEs), 6) the 'Pathoresources' topic (*how to build and leverage technological innovation and resources to better understand plant-pathogen interactions?*; 53 HIPEs), and 7) the 'General review' topic (*how do we conceptually understand the role of effectors in plant-pathogen interactions?*; 39 HIPEs) (see [Supplementary Text](#) for details). Interestingly, the annual citation rate is comparable between these main research topics ([Supplementary Figure S3](#)).

To gain a more accurate understanding of HIPEs research questions, we further grouped HIPEs into 20 sub-topics ([Figure 2](#)). Thus, each of the

seven main research topics comprises two to five sub-topics that pertain to a more specific research question. For example, the ETI topic comprises two sub-topics: 'Immune receptors' (*what are the receptors that recognize effectors?*) and 'Effector recognition' (*how do immune receptors recognize effectors and signal*

that recognition?). Overall, these sub-topics highlight several specific research questions and the main addressed are: '*what is the function of pathogenic effectors in the host?*' (18% of HYPEs, ETS topic) and '*how do we develop and use omics data to identify pathogenic effectors?*' (16% of HYPEs, Pathoresources topic).

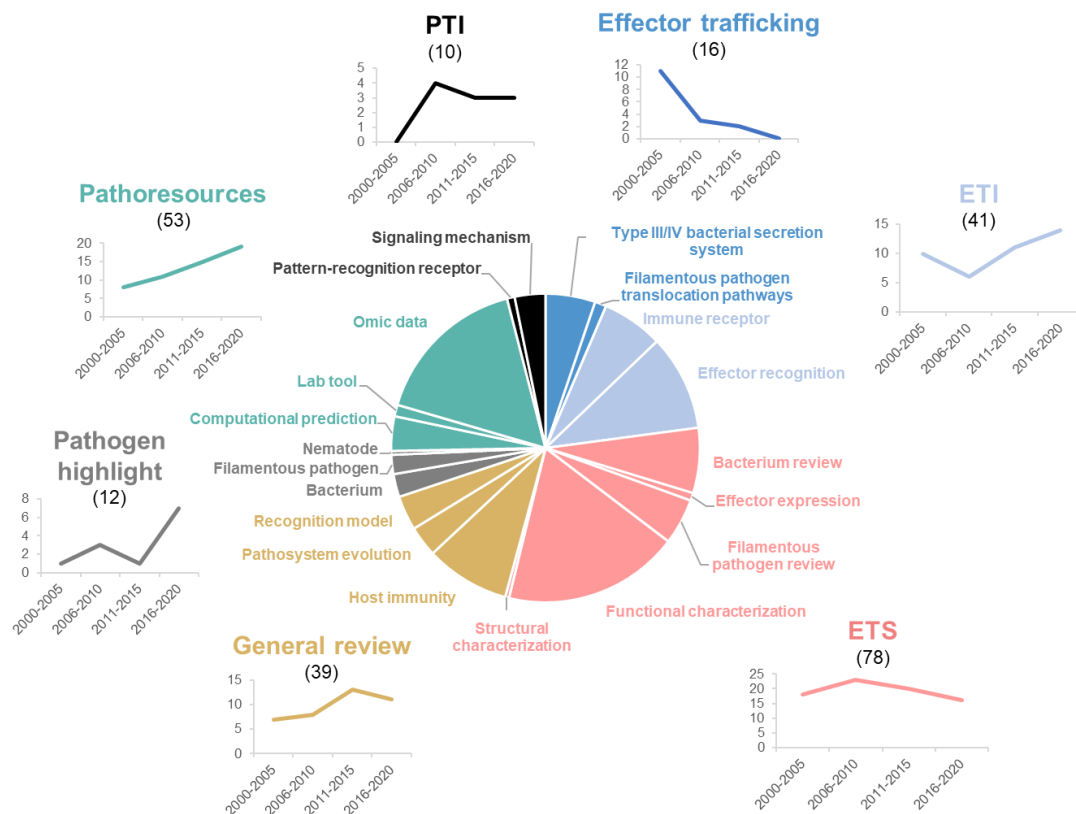


Figure 2. HYPEs pertain to seven main research topics

Pie chart displaying the seven main research topics and 20 sub-topics addressed by the HYPEs and their publication trends over time. The main research topics, sub-topics and trendlines associated are color-coded as indicated in Figure S3. Research sub-topics are indicated as separated pie segments within a main topic. The categorization of each HYPEs was based on iterative expert reading and key word association of the entire HYPE collection. Numbers above the main research topics indicate the total number of HYPEs for each topic. Trendlines indicate the number of HYPEs for each topic according to four five-year time frames: 2000-2005; 2006-2010; 2011-2015 and 2016-2020. PTI: PAMP-triggered immunity; ETI: Effector-triggered immunity; ETS: Effector-triggered susceptibility. The raw data used to build this figure are available in the [Dataset 1](#).

To identify potential research trends within the HYPEs, we analyzed the evolution of the number of publications in each of the seven main topic between 2000 and 2020, by five-year time frames (*i.e.* 2000-2005, 2006-2010, 2011-2015, and 2016-2020). That analysis showed that most topics remain stable over time. In contrast, the two topics Effector trafficking and Pathoresources showed marked trends of

decrease and increase over time, respectively. The Effector trafficking topic declined markedly over the years, mainly due to the reduction of HYPEs addressing the bacterial Type III or Type IV secretion system. The strong controversy on the mechanisms of delivery of filamentous pathogen effectors may also explain the decline of this topic (Anderson *et al.*, 2015; Tyler *et al.*, 2013; Wawra *et al.*, 2013; Wawra *et al.*, 2017).

At the opposite, the Pathoresources topic steadily increased, probably benefiting from the progresses in genomics that helped the identification of candidate effectors (Figure 2). In conclusion, this set of analyses show that HYPEs pertain to key research questions that address well-defined aspects of the molecular interaction between plants and pathogens; the relative importance of some of those increased (*i.e.* Pathoresources) or declined (*i.e.* Effector trafficking) over the last two decades.

HYPEs address a handful of key organisms and proteins

To identify the main objects (*i.e.* organisms or molecules) investigated by the HYPEs, we performed a word occurrence analysis of the title and abstracts combined with word cloud generation and iterative text enrichment for words referring to organisms or molecules

(Dataset 2; see Supplementary Methods for details). That pipeline helped to generate a world cloud of the 200 most frequently used words referring to organisms or molecules (Figure 3A). As expected, the most used words refer to key groups of organisms (pathogen, *Arabidopsis*, bacterium, fungus, *Pseudomonas*) or groups of molecules (effector, receptor, NLR, gene, protein, genome). We further quantitatively analyzed Dataset 2 to identify the top five most frequently referred to plant species, pathogen species, immune receptors, and effectors (Figure 3B-E). Firstly, the top five model plants comprise a Brassicaceae (*Arabidopsis thaliana*), two Poaceae (*i.e.* cereals; rice and wheat), and two Solanaceae (potato and tomato). The fact that three out of these five model plants are key crops providing staple food worldwide (*i.e.* rice, wheat, and potato; Savary *et al.*, 2019) shows the alignment of research efforts with agricultural efforts to meet global food security (Figure 3B).

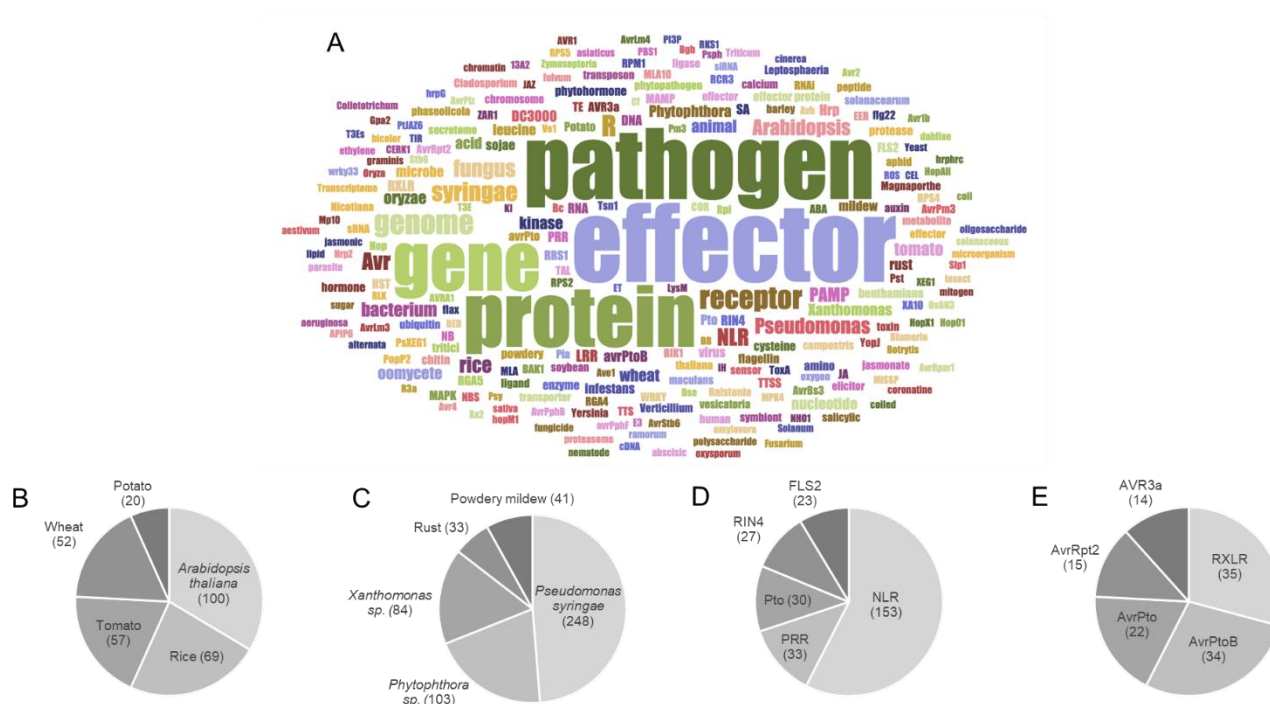


Figure 3. HYPEs rely on a handful of model organisms and proteins

(A) Word cloud displaying the most frequent words referring to organisms or molecules in the title and abstract of the HYPEs. The word cloud was built using a filtered text file including HYPEs metadata (publication title and abstract) deprived from words that did not explicitly refer to organisms or molecules. Word colors were randomly generated to assist visual word discrimination. The word cloud displays 200 words. The size of the words positively correlates with their frequency in the text file. A top five of plant organisms (B), plant-associated pathogens (C), immune receptors (D) and pathogen effectors (E) was identified based on the Dataset 2. Specific additional key words were considered for the following topics: *Arabidopsis thaliana* ('*Arabidopsis*' and '*thaliana*'), *Pseudomonas syringae* ('*Pseudomonas*', '*syringae*', 'DC3000' and 'pst'), *Phytophthora sp.* ('*Phytophthora*', '*infestans*', '*ramorum*' and '*sojae*'), *Xanthomonas sp.* ('*Xanthomonas*', '*campestris*' and '*oryzae*' if used in a

meaningful context), Powdery mildews ('Powdery' and 'mildews'), NLR ('NLR', 'LRR', 'NB-LRR', 'TNL', 'CNL', 'sNLR' and 'hNLR'). NLR: nucleotide-binding/leucine-rich-repeat receptor; PRR: pattern recognition receptors. The raw data used to build this figure are available in the [Dataset 2](#).

Secondly, the top five model pathogens comprise two bacteria (*Pseudomonas syringae* and *Xanthomonas* species), two groups of fungi (Pucciniales and Erysiphales, causing rust and powdery mildew diseases), and one genus of oomycetes (*Phytophthora* species) ([Figure 3C](#)). These pathogens collectively cause a wide range of diseases that significantly impact agricultural production worldwide (Fones *et al.*, 2020; Savary *et al.*, 2019). Thirdly, the top five model receptors comprise two general groups of immune receptors (NLRs and PRRs), as well as three specific proteins: FLS2 (the PRR responsible for flagellin recognition), Pto (a cytosolic kinase), and RIN4 (a regulator of immunity). The prominence of NLRs mirrors their importance in ETI, and the importance of ETI as a research topic within HIPEs ([Figure 3D](#)). Finally, the top five model groups of effectors comprise three *P. syringae* effectors (AvrPto, AvrPtoB, and AvrRpt2) and two oomycete effector families (the RXLR superfamily, and the AVR3a family) ([Figure 3E](#)). Altogether, these analyses reveal the prominence of *A. thaliana*, *P. syringae*, as well as receptor and effector gene families as model objects in effector biology. We refer readers to [Supplementary Text](#) for a more detailed and contextualized analysis of the organisms and molecules listed above.

Temporal analysis of model pathogens reveals the increasing importance of plant pathogenic fungi

To get a more detailed understanding of the model pathogens addressed in HIPEs, we performed an iterative analytical reading of all HIPEs and categorized them according to the taxonomic group of the pathogens they emphasized (if any). This analysis revealed that 80% of the HIPEs emphasize a specific pathogen; we grouped those HIPEs into six

categories: bacteria (96 HIPEs), fungi (74), oomycetes (33), viruses (3), nematodes (2), and aphids (1) ([Dataset 1](#)) ([Figure 4A](#)). Only a handful of HIPEs emphasize aphids, viruses and nematodes, suggesting that the effector biology community revolves mostly around bacterial, fungal and oomycete model systems. Notably, the categories bacteria of oomycetes (33% and 13% of the collection, respectively) show low diversity, as they mostly address *Pseudomonas* and *Phytophthora* species, respectively ([Dataset 1](#)). In contrast, the fungal group (28% of the HIPEs) shows a high diversity, as it addresses 15 different fungal genera ([Dataset 1](#)). This indicates that bacteria and oomycete groups are dominated by a limited number of key model species, while the fungal group addresses a broader diversity of species. Interestingly, the size of the categories evolved drastically between 2000 and 2020 ([Figure 4B](#)). Indeed, between the 2000-2005 and the 2016-2020 time periods, studies focusing on bacteria declined from 75% to 21% of the HIPE collection, while studies focusing on oomycetes and fungi increased from 2% to 13% and from 2% to 40%, respectively. These results indicate that in the early 2000s model bacterial systems vastly dominated effector biology, but that over time filamentous pathogens (*i.e.* fungi and oomycetes) gained importance. This likely reflects the impact of pathogenomics and the possibility for systematic effectors prediction in sequenced genomes of a larger number of microbes, particularly fungi.

The influence of publications addressing fungal effectors increased over time: analysis of the 'HIPE-fun' collection

To perform an objective analysis of the most prominent fungal species in influential publications addressing fungal plant pathogen effectors, we repeated the bibliometric analysis

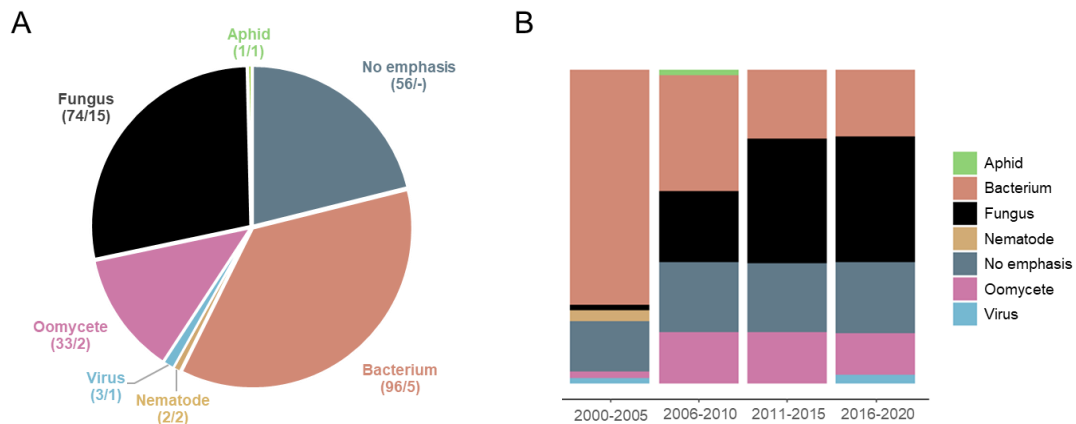


Figure 4. Studies emphasizing fungi gain importance over time.

(A) Pie chart displaying the seven taxonomic groups of pathogens emphasized (if any) addressed by the HIPEs. The assignment of each HIPE was based on iterative expert reading of the publications. For each taxonomic group, the number of HIPEs and the total number of species are indicated (e.g. '74/15'). (B) Percent stacked bar chart displaying the evolution of the relative size of taxonomic groups over four five-year time periods: 2000-2005; 2006-2010; 2011-2015 and 2016-2020. Color code is the same as in (A). The raw data used to build this figure are available in the [Dataset 1](#).

that identified the HIPE collection, by considering only the research articles on fungi. This helped to build a collection of 100 HIPEs focusing on fungi (thereafter referred to as 'HIPE-funs'; [Dataset 3](#); see [Supplementary Methods](#) and [Supplementary Figure S2](#) for details), archived on the following public web address: https://www.zotero.org/groups/441090/5/hipe-fun_collection/library.

To understand the expansion of publications focus on fungi in HIPEs, we extracted the number of publications addressing plant pathogen effectors and the citation rank over years of the HIPE-funs (i.e. rank of the publication on the Web of Science database based on the number of citations). This analysis highlighted an obvious increase in the citation rank over years of the HIPE-funs associated with the expansion in the number of publications addressing plant pathogen effectors. Between 2000-2005 and 2016-2020, studies on fungi were ranked on average from 33rd place out of 56 publications to 7th place out of 192 publications ([Figure 5A](#)). This result displays the significant increase in the influence of publications related to fungi over time, and more precisely by two predominant trophic lifestyles: biotrophy and hemibiotrophy (45% for both; [Figure 5B](#)).

The HIPE-funs are related to influential fungal species in the field of molecular plant pathology

In 2012, Dean and colleagues surveyed hundreds of mycologists who voted for the most important fungal species in molecular plant pathology based on their scientific and economic importance (495 votes in total). We performed a comparative analysis to evaluate the correspondence between the fungal species addressed in HIPE-funs and the top 10 list from Dean et al. (2012). We first identified a total of 21 fungal genera covered in the HIPE-funs. We ranked fungal genera according to HIPE-funs numbers and annual citation rates, and then we compared this ranking with the list by Dean and colleagues ([Table 2](#)). First, this analysis showed that all top 10 species occur in at least one HIPE-fun, highlighting an excellent correspondence between the two lists ([Dataset 3](#)). Notably, the genera *Magnaporthe* and *Puccinia* appear in the top of both lists ([Table 2](#); Dean et al., 2012). These genera comprise species that trigger dramatic epidemics on rice and/or wheat, threatening global food security (Figuerola et al., 2018; Talbot, 2003; Wilson and Talbot, 2009). That may explain why they represent important fungal models in the field of fungal effector

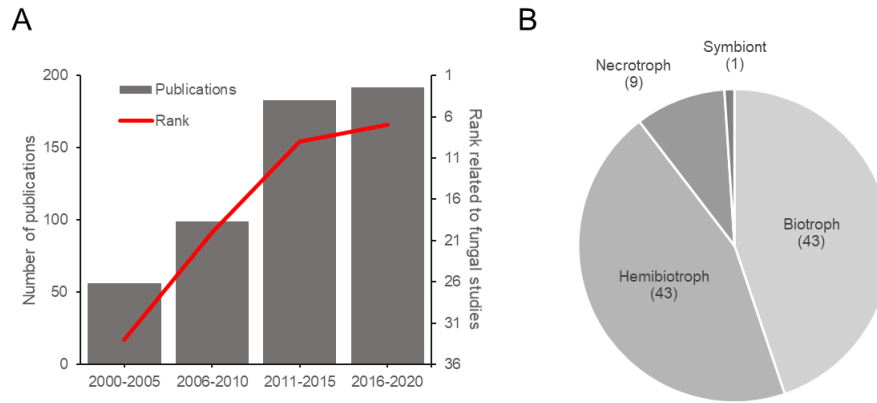


Figure 5. Publications addressing effectors of (hemi)biotrophic fungi gain prominence over time.

(A) Evolution of the number of publications related to plant pathogen effectors and the citation rank for HIPE-funs. Each citation rank was calculated based on the mean of rank of publications by time frames (*i.e.* position of the publication on the Web of Science website based on the number of citations). (B) Pie chart displaying the proportion of each lifestyle of plant pathogenic fungi studied in the HIPE-funs. The categorization of each lifestyle was based on iterative expert reading and association with the pathogenic species studied for the entire HIPE-fun collection. Numbers above lifestyle topics indicate the total number of HIPE-funs for each topic. The raw data used to build this figure are available in the [Dataset 3](#).

biology. In contrast, the ranking of some species differs between the two lists. For instance, the genus *Botrytis sp.* dominates the top 10 list of Dean et al. (2012), but it is barely represented in the HIPE-funs (2nd place in the previous report vs. 13th place in this study; [Table 2](#)). This genus, and notably the species *Botrytis cinerea*, is a strong model for molecular plant pathology but not in effector biology. This is probably because

of its necrotrophic lifestyle (poorly represented by the HIPE-funs; [Figure 5B](#)); a lifestyle that is though not to rely much on effectors during host infection, but rather on toxins. To conclude, our analysis of HIPE-funs confirms the importance of well-established fungal pathogens as agronomical models in both effector biology and molecular plant pathology.

Table 2. Main fungal plant pathogens with the highest number of publications and annual citations based on HIPE-funs.

Fungal pathogen	Rank	Number of publications	Citation rate (per year)	Rank based on Dean <i>et al.</i> , 2012 top 10 list
<i>Blumeria sp.</i>	1	12	240	6
<i>Magnaporthe sp.</i>	2	10	206	1
<i>Leptosphaeria sp.</i>	3	10	136	-
<i>Cladosporium sp.</i>	4	9	171	-
<i>Puccinia sp.</i>	5	9	73	3
<i>Verticillium sp.</i>	6	6	163	-
<i>Melampsora sp.</i>	7	6	121	10
<i>Zymoseptoria sp.</i>	8	6	117	7
<i>Fusarium sp.</i>	9	6	84	4 & 5
<i>Colletotrichum sp.</i>	10	4	124	8
<i>Ustilago sp.</i>	11	4	87	9
<i>Sclerotinia sp.</i>	12	4	67	-
<i>Botrytis sp.</i>	13	2	117	2

Conclusion and outlook

To conclude, the present study shows that top tiers plant effector biology has developed as a well-structured research area, with key academic actors and objects (*i.e.* molecules or organisms). The study also reveals that the focus of the most cited publications in the field has partially shifted over time, from bacterial pathogens to filamentous pathogens (notably fungi). As an outlook for the next twenty years, we anticipate that the research area will continue to diversify the organisms it addresses (*i.e.* aphids, herbivores, viruses), which may help understand better the diversity of virulence strategies that arose throughout evolution.

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Authors contribution

CL acquired data and wrote the manuscript. CL performed data analysis and interpretation, with inputs from BP and SD. All authors conceived and designed the study, as well as critically revised and edited the manuscript.

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Conflict of Interest

The authors declare that there is no conflict of interest.

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SUPPLEMENTARY METHODS

Building of the HIPE and HIPE-fun collections

To identify and extract publications in plant pathogen effectors that have been published between 2000 and 2020 and that have been highly cited, we used a step-by-step pipeline that used the Web of Science website as described previously by Petre et al. (2021), with the following modifications. We used the Mendeley software instead of Zotero. We selected publications following searches with three groups of keywords: 'plant pathogen effector', 'plant pathogen avirulence effector' and 'plant pathogen virulence effector'. We defined 12-time periods (2000-2001; 2002-2003; 2004-2005; 2006-2007; 2008-2009; 2010-2011; 2012-2013; 2014-2015; 2016-2017; 2018; 2019; 2020). The last three years have been considered separately due to low citation numbers (grouping them in pairs would have excluded publications from the most recent year). Three publications per year were considered (*e.g.* we selected six publications for the time period 2000-2002 and only three publications for the year 2020). In order to import all the metadata of the publications (*e.g.* PDF, title, abstract, author list, journal, ...), we used the 'Mendeley Web Importer' tool. Finally, we removed all redundant publications between the three different extraction to obtain a collection of 249 non-redundant publications (HIPE collection). In addition, we reperformed this step-by-step pipeline included all variations cited above in order to extract a corpus of 100 research articles focused only on fungal pathogens (HIPE-fun collection). We archived both HIPE and HIPE-fun collections in a public Mendeley web folder as follow: 'HIPE collection' (https://www.zotero.org/groups/4410902/hipe_collection/library) and 'HIPE-fun collection' (https://www.zotero.org/groups/4410905/hipe-fun_collection/library).

Categorization of publications into research topics and organisms studied

To group HIPEs according to their research topics, we performed an iterative analytical reading of the publications and keywords aimed

at identifying their main research questions and the organism studied, as described previously (Petre *et al.*, 2021). Throughout this process, we grouped the HIPEs into (i) topics and subtopics according to the main research and specific questions they address or (ii) the pathogenic organisms or group of pathogenic organisms addressed by HIPEs ([Dataset 1](#)). In addition, to evaluate the temporal distribution of the HIPEs within each group cited above, we quantified their number per five-year time frames: 2000-2005, 2006-2010, 2011-2015 and 2016-2020.

Generation of word clouds and analysis of key organisms and molecules

To analyze text content, we built the text files using Microsoft Excel and Text Wrangler softwares, as described previously (Petre *et al.*, 2021). We first manually copied and pasted the relevant text from Mendeley metadata (publication title and abstract) into a Microsoft Excel spreadsheet ([Dataset 1](#)) and we then generated the word clouds containing only words referring to organisms and molecules with filtered text files ([Dataset 2](#)). An accurate quantification of the most frequent words was performed using the online WordClouds generator (<https://www.wordclouds.com/>). To generate Excel spreadsheets with the word occurrences, we imported our filtered text files and we used the 'Word list' function to export them.

SUPPLEMENTARY MATERIAL

Figure S1

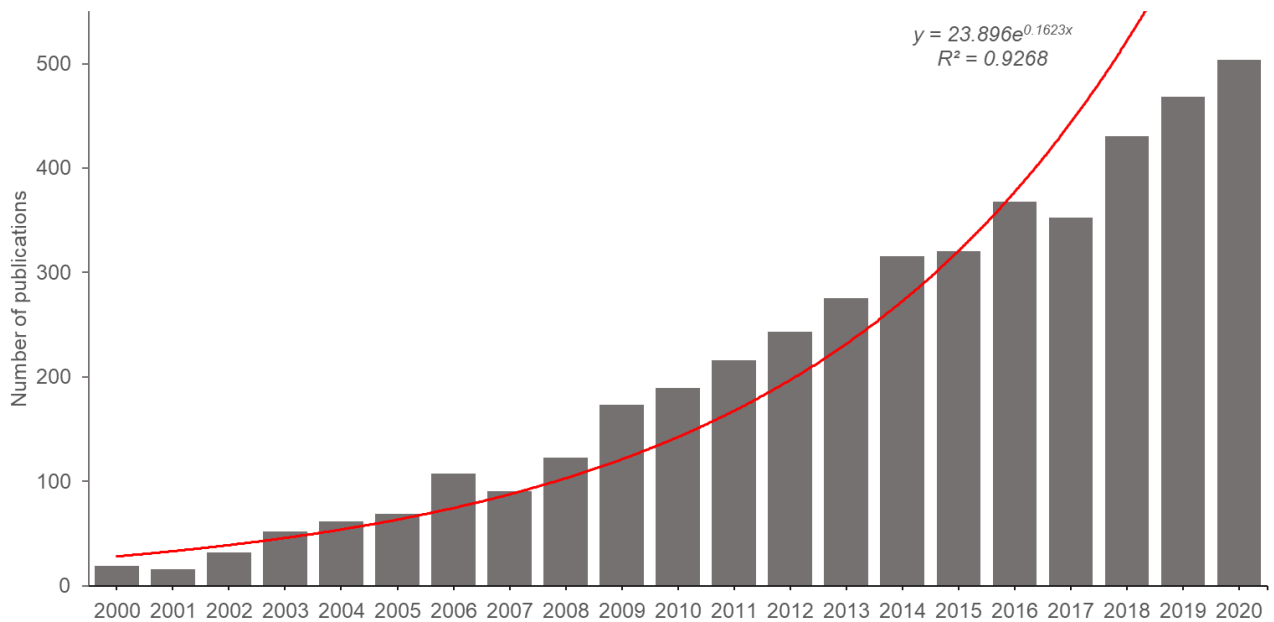


Figure S1. The number of publications pertaining to plant pathogen effectors increases exponentially over time.

Figure S2

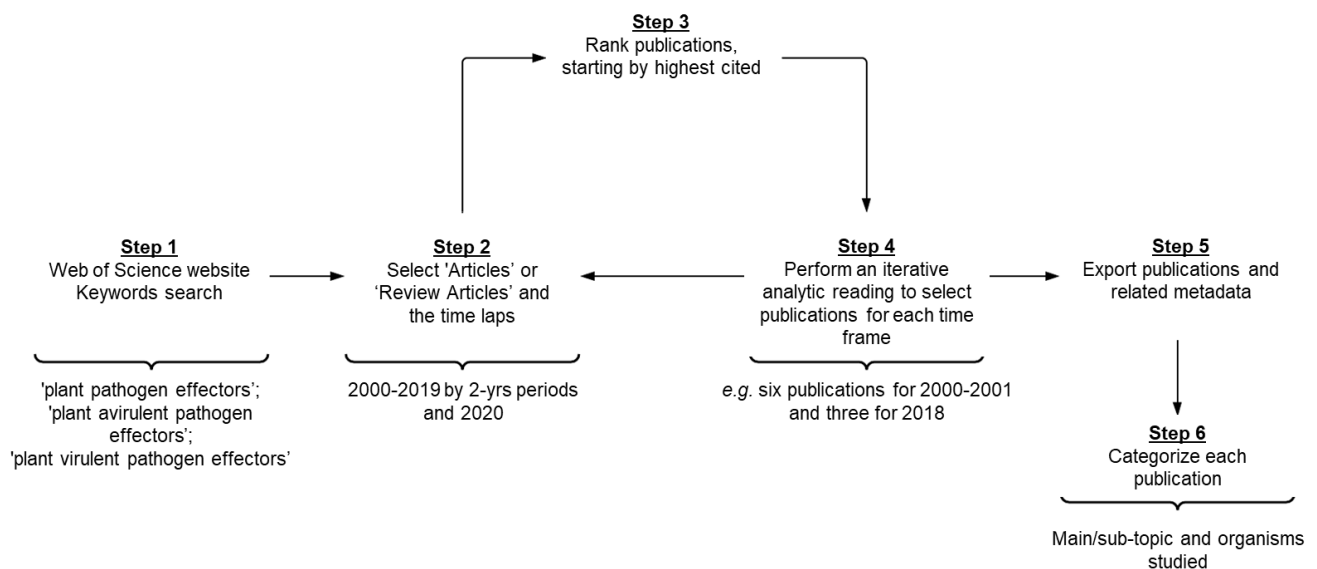


Figure S2. Operational diagram displaying the step-by-step pipeline used to build the HIPE and HIPE-fun collections.

Figure S3

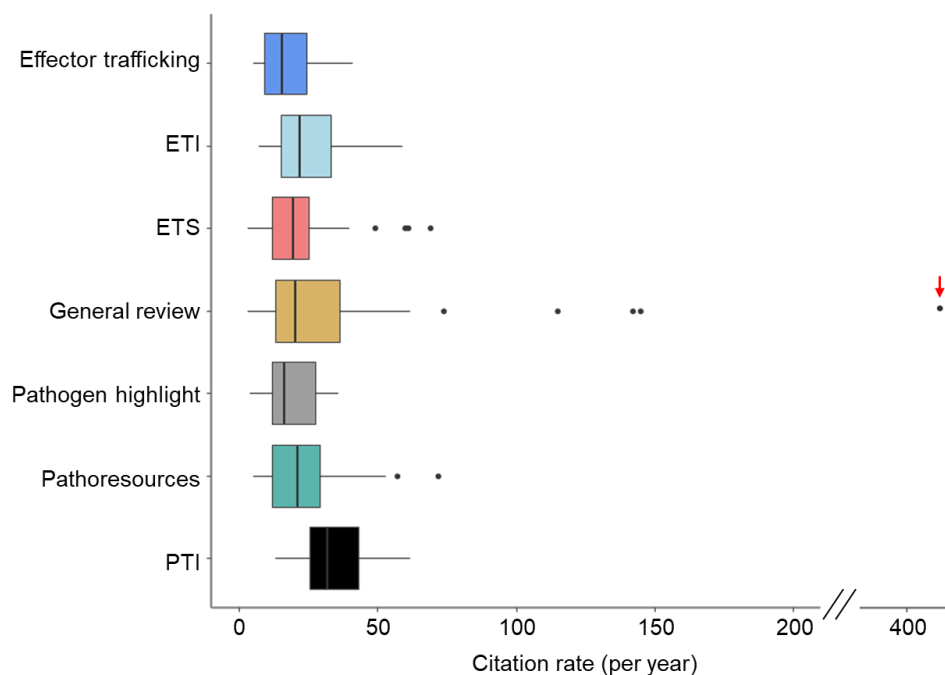


Figure S3. The seven main research topics show comparable citation rates.

Boxplots indicating the annual citation rate of the seven main research topics addressed by the HYPEs. The red arrow indicates the HYPE with the highest annual citation rate, which corresponds to the 2006 review by Jones and Dangl that presented the seminal zig-zag model of the plant immune system. The raw data used to build this figure are available in the [Dataset 1](#).

Dataset 1. Raw dataset including the 249 HYPEs and main meta data.

Dataset 2. Filtered text file of the 249 HYPE titles and abstracts.

Dataset 3. Raw dataset including the 100 HYPE-funs and main meta data.

SUPPLEMENTARY TEXT

Effector trafficking topic studies how pathogens secrete effectors in the host

The 'Effector trafficking' topic comprises 16 publications (six research articles and ten reviews) that collectively gathered around 4.4k citations. Among them, bacterial studies predominate, as only three publications focused on filamentous pathogens. The topic comprises two subtopics. The 'Type III/IV bacterial system' subtopic comprises 13 publications. The majority address the current knowledge on the Type III secretion system (TTSS) and associated effectors (Alfano and Collmer, 2004; Büttner and Bonas, 2002a; Büttner and Bonas, 2002b; Cornelis and Van Gijsegem, 2000; Galán *et al.*, 2014; He *et al.*, 2004; Jin *et al.*, 2003; Lindeberg *et al.*, 2012) and the Type IV secretion system (Christie, 2001; Christie and Vogel, 2000). On another hand, three publications describe and analyze how *hrp/hrc* genes encode the Hrp (type III secretion) system and other putative effectors as well as its associated secretion mechanisms (Alfano *et al.*, 2000; Collmer *et al.*, 2000; Lee *et al.*, 2001). The 'Filamentous pathogen translocation pathways' subtopic comprises three publications. One publication addresses the functioning of the biotrophic interfacial complex (BIC) of *Magnaporthe oryzae* (Khang *et al.*, 2010), and two publications focus on how effectors traffic to the host cell cytosol (Whisson *et al.*, 2007) (Kale *et al.*, 2010).

ETI (Effector-triggered immunity) topic highlights the immune resistance with the specific recognition of effectors

The 'ETI (Effector-triggered immunity)' topic comprises 41 publications (30 research articles and 11 reviews) that collectively gathered around 9.7k citations. Near 76% of those publications emphasize a specific organism (or group of organisms), including notably fungi and bacteria (41 and 27%, respectively). This topic comprises two subtopics. The 'Immune receptor' subtopic comprises 17 publications that summarize and discuss recent findings on the diversity, the structure, and the function of NLRs (nucleotide-binding leucine-rich repeat receptors) (Bai *et al.*, 2012; Belkhadir *et al.*, 2004; Cesari *et al.*, 2014; DeYoung and Innes, 2006; Jubic *et al.*, 2019; Lu *et al.*, 2016; Marchal *et al.*, 2018; Martin *et al.*, 2003; McHale *et al.*, 2006; Pedley and Martin, 2003; Saintenac *et al.*,

2018; Shen *et al.*, 2007; van Der Vossen *et al.*, 2000; Wang *et al.*, 2019a; Wang *et al.*, 2019b; Williams *et al.*, 2014) or compare plant and animal immune systems (Maekawa *et al.*, 2011). The 'Effector recognition' subtopic comprises 24 publications. The first set of publications addresses direct and indirect recognition of pathogens by the plant immune system (Ellis *et al.*, 2007; Kourelis and Van Der Hoorn, 2018; Petit-Houdenot and Fudal, 2017). A second set is focused on the direct recognition model following the gene-for-gene model (Allen *et al.*, 2004; Bourras *et al.*, 2015; Bourras *et al.*, 2019; Dodds *et al.*, 2006; Gu *et al.*, 2005; de Jonge *et al.*, 2012; Navathe *et al.*, 2020; Paulus *et al.*, 2020; Saur *et al.*, 2019; Vleeshouwers *et al.*, 2011; Yang *et al.*, 2006). The last set of publications studies the indirect recognition of pathogen effectors (Tian *et al.*, 2014) following the guard model (Axtell and Staskawicz, 2003; Deslandes *et al.*, 2003; Mackey *et al.*, 2002; Shao *et al.*, 2003) and finally the recognition mediated by NLR-ID following the decoy model (Cesari *et al.*, 2013; Kroj *et al.*, 2016; Le Roux *et al.*, 2015; Sarris *et al.*, 2015; Sarris *et al.*, 2016).

ETS (Effector-triggered susceptibility) topic explains how pathogens deploy effectors to promote infection disease

The 'ETS (Effector-triggered susceptibility)' topic comprises 78 publications (45 research articles and 33 reviews) that collectively gathered around 17k citations. Nearly 94% of those publications emphasize a specific or a group of organisms with a preponderance of bacterial studies in contrast to studies focused on filamentous pathogens (60 and 40%, respectively). This topic comprises five subtopics. The 'Bacteria review' subtopic comprises 17 publications. A first well-defined set of publications summarizes our knowledge on Type III bacterial effectors (Boch and Bonas, 2010; Büttner, 2016; Greenberg and Vinatzer, 2003; Gürlebeck *et al.*, 2006; Macho, 2016; Macho and Zipfel, 2015; Oh and Beer, 2005; Winstanley and Hart, 2001). Another set of publications reviews the recent investigations on intricate molecular interactions with bacterial elicitation and evasion of plant innate immunity (Abramovitch *et al.*, 2006; Deslandes and Rivas, 2012) and comprises comparative analyses with the fungal pathogens (Hogenhout *et al.*, 2009;

Khan *et al.*, 2018) or animal-specific bacteria (Büttner and Bonas, 2003; Orth, 2002). One publication studies the impact of auxin on pathogenesis and during the interactions with bacterial pathogens (Kunkel and Harper, 2018). Finally, a last set of publications summarize researches on the infection pathways of the genus *Xanthomonas* sp. (Büttner and Bonas, 2010) and more precisely the contribution of transcription activator-like effectors (TALEs) (Perez-Quintero and Szurek, 2019). The 'Effector expression' subtopic comprises two publications and highlights the epigenetic regulation of effector gene expression in the fungus *Leptosphaeria maculans* (Soyer *et al.*, 2014) and the regulation of the *hrp* gene cluster encoding the type III protein secretion system (TTSS) (Noël *et al.*, 2001). The 'Filamentous pathogen review' subtopic comprises 12 publications reviewing the recent findings on fungal effectors (Anderson *et al.*, 2015; Franceschetti *et al.*, 2017; Giraldo and Valent, 2013; Han and Kahmann, 2019; Lo Presti *et al.*, 2015; de Sain and Rep, 2015; Selin *et al.*, 2016; Stergiopoulos *et al.*, 2013; Stergiopoulos and de Wit, 2009; Tsuge *et al.*, 2013), on oomycete effectors (Schornack *et al.*, 2009), and on the use of effectors as cellular probes (Toruño *et al.*, 2016). The 'Functional characterization' subtopic comprises 46 publications. Nearly 71% of those publications study the modulation of immune responses by effectors (Bos *et al.*, 2006; Feng *et al.*, 2012; Gao *et al.*, 2019; Gimenez-Ibanez *et al.*, 2009; Göhre *et al.*, 2008; Hou *et al.*, 2019; Houterman *et al.*, 2008; Kim *et al.*, 2005; Li *et al.*, 2005; Mackey *et al.*, 2003; Nomura, 2006; Park *et al.*, 2012; Rooney, 2005; Wang *et al.*, 2016; Weiberg *et al.*, 2013; Xia, 2004; Xiang *et al.*, 2008; Zhang *et al.*, 2007; Zhang *et al.*, 2010), compare bacterial and fungal modulation of plant immunity (Göhre and Robatzek, 2008), address phytohormone modulation (Gimenez-Ibanez *et al.*, 2014; Kazan and Lyons, 2014; Liu *et al.*, 2014; Plett *et al.*, 2014), or focus on plant trafficking modulation (Aung *et al.*, 2020; Brooks *et al.*, 2005; Chen *et al.*, 2010; DebRoy *et al.*, 2004; de Jonge *et al.*, 2010; Kay *et al.*, 2007; Mentlak *et al.*, 2012; Orth, 2000; Shan *et al.*, 2008; de Torres-Zabala *et al.*, 2007). A second set of publications identifies avirulence genes and validates their Avr activity (Tsiamis *et al.*, 2000; Zhong *et al.*, 2017) and highlights the masking model as a counter-defense of pathogen to evade the immune system (Ma *et al.*, 2017; Plissonneau *et al.*, 2016). Five publications

characterize the activity of type III bacterial effectors (Abramovitch *et al.*, 2003; Abramovitch and Martin, 2005; He *et al.*, 2006; Jamir *et al.*, 2004; Nimchuk *et al.*, 2000) and the associated environmental influences (Xin *et al.*, 2016). Finally, two publications study the virulence activity and virulent motifs of effectors secreted by the soybean pathogen *Phytophthora sojae* (Dou *et al.*, 2008; Ma *et al.*, 2015). The 'Structural characterization' subtopic comprises one publication that reports the crystal structure of the TALE PthXo1 of *Xanthomonas oryzae* (Mak *et al.*, 2012).

General review topic conceptualizes our knowledge on plant-pathogen interactions

The 'General review' topic comprises 39 publications (all reviews) that collectively gathered around 18k citations. Nearly 77% of those publications do not emphasize on a specific or a group of organisms. It comprises three subtopics. The 'Host immunity' subtopic comprises 22 publications. A first series of nine publications summarizes recent findings on ETI (Cui *et al.*, 2015; Thordal-Christensen, 2020; Wu *et al.*, 2014), PTI (PAMP-triggered immunity) (Boller and Felix, 2009; Hématy *et al.*, 2009), compares them (Chisholm *et al.*, 2006; Dodds and Rathjen, 2010; Liu *et al.*, 2013; Qiu *et al.*, 2008; Thomma *et al.*, 2011; Tsuda and Katagiri, 2010), or emphasize some taxonomic groups (Liu *et al.*, 2014; Zvereva and Pooggin, 2012). The other set of publications describes the contribution of phytohormones to plant immunity (Zhang and Li, 2019), the regulation and the signaling pathways of host immunity (Feys and Parker, 2000; Hacquard *et al.*, 2017; Wang *et al.*, 2020), the antiviral immunity (Calil and Fontes, 2017; Gouveia *et al.*, 2017), the defense priming (Conrath, 2011), or the non-host resistance in plant (Nürnberger and Lipka, 2005). Finally, two publications compare immunity between plants and animals (Staskawicz *et al.*, 2001) and between bacteria and fungi (van't Slot and Knogge, 2002). The 'Pathosystem evolution' subtopic comprises eight publications that summarize our knowledge on evolutionary models and mechanisms of plant-pathogen interactions (Brown and Tellier, 2011; Dong *et al.*, 2015; Frantzeskakis *et al.*, 2019; Raffaele and Kamoun, 2012; Schulze-Lefert and Panstruga, 2011) with a focus on climate change (Velásquez

et al., 2018) and R-Avr (Resistance gene – Avirulence gene) interactions (Białas *et al.*, 2018). Finally, one publication compares the evolution in bacterial and fungal pathosystems (Dou and Zhou, 2012). The 'Recognition model' subtopic comprises nine publications and proposed different conceptual models focused on the plant immune system (Bent and Mackey, 2007; Bonas and Lahaye, 2002; van Der Hoorn and Kamoun, 2008; Jones and Takemoto, 2004; Jones and Dangl, 2006; Nimchuk *et al.*, 2001; Stotz *et al.*, 2014) and comparative analyses with the animal immune system (Jones *et al.*, 2016). Finally, one publication summarizes specifically bacterial recognitions models (Khan *et al.*, 2016).

Pathogen highlight topic emphasizes on specific organisms

The 'Pathogen highlight' topic comprises 12 publications (all reviews) that collectively gathered around 1.6k citations. These reviews emphasize bacteria (6), fungi (4), oomycetes (1) and nematodes (1). It comprises three subtopics. The 'Bacterium' subtopic comprises six publications and summarize recent findings on the genera *Xanthomonas* (An *et al.*, 2020; Kumar *et al.*, 2020; Niño-Liu *et al.*, 2006; Timilsina *et al.*, 2020) and *Pseudomonas* (Xin *et al.*, 2018; Xin and He, 2013). The 'Filamentous pathogen' subtopic comprises five publications and summarize recent findings on the oomycete *Phytophthora infestans* (Fry, 2008), the fungus *Cladosporium fulvum* (de Wit, 2016), the rust fungi (Lorrain *et al.*, 2019), the mycorrhizal fungi (Genre *et al.*, 2020) and an overview of selected fungal species with a focus on PAMPs and associated effectors (de Wit *et al.*, 2009). The 'nematode' subtopic comprises one publication on the model species *Caenorhabditis elegans* (Alegado *et al.*, 2003).

Pathoresources uses omics approaches and technological innovations to study plant-pathogen interactions

The 'Pathoresources' topic comprises 53 publications (42 research articles and 11 reviews) that collectively gathered around 11k citations. It comprises three subtopics. The 'Omic data' subtopic comprises 41 publications. Almost half of those publications provides genomic data (Baltrus *et al.*, 2011; Buell *et al.*, 2003; Cooke *et al.*, 2012; Dale *et al.*, 2019; Duan *et al.*, 2009; Faino *et al.*, 2016; Genin and

Boucher, 2004; Genin and Denny, 2012; Grandaubert *et al.*, 2014; Haas *et al.*, 2009; Joardar *et al.*, 2005; Kema *et al.*, 2018; Laflamme *et al.*, 2020; Levy *et al.*, 2018; Li *et al.*, 2020; O'Connell *et al.*, 2012; Rouxel *et al.*, 2011; Salanoubat *et al.*, 2002; Spanu *et al.*, 2010; Thieme *et al.*, 2005; Tyler *et al.*, 2006; Wyatt *et al.*, 2020; Yoshida *et al.*, 2009) and four publications perform comparative analyses of genomic data (Fouché *et al.*, 2018; Fouché *et al.*, 2020; Spanu, 2012; de Wit *et al.*, 2012). A second set of publications reports effectoromic analyses (Jiang *et al.*, 2008; Vleeshouwers *et al.*, 2008), secretomic analyses (Bos *et al.*, 2010; Kamoun, 2006; Kamoun, 2007; Poueymiro and Genin, 2009; Vincent *et al.*, 2020), transcriptomic analyses (Rudd *et al.*, 2015; Wang *et al.*, 2011) and studies of the effector-target interactome network (Mukhtar *et al.*, 2011; Weßling *et al.*, 2014). Finally, three publications describe the pathogen–host interactions database (PHI-base) providing curated molecular and biological information on gene catalogues associated with pathogen–host interactions (Urban *et al.*, 2015; Urban *et al.*, 2017; Urban *et al.*, 2020). The 'Lab tool' subtopic comprises three publications and describe molecular genetic tools to enhance lab investigations for a better comprehension of plant-pathogen interactions (Fang and Tyler, 2016; Ghislain *et al.*, 2019; Nowara *et al.*, 2010). Finally, the 'Computational prediction' subtopic comprises nine publications which describe pipelines to identify and characterize effectors of filamentous pathogens (Saunders *et al.*, 2012; Sperschneider *et al.*, 2016; Sperschneider *et al.*, 2017; Sperschneider *et al.*, 2018a; Sperschneider *et al.*, 2018b), of bacteria (Chang *et al.*, 2005; Collmer *et al.*, 2002; Lindeberg *et al.*, 2005), or to annotate NLRs (Steuernagel *et al.*, 2020).

PTI topic describes the basal disease resistance of plant

The 'PTI' topic comprises ten publications (four research articles and six reviews) that collectively gathered around 2.7k citations. Among them, five publications do not focus on a specific organism or a group of organisms, four study specifically focus on a bacterium and only one on a fungus. It comprises two subtopics. The 'Pattern-recognition receptor' (PRR) subtopic comprises two publications. These two reviews summarize and discuss recent findings on plant PRRs, their diversity to recognize different

ligands, and the ability of pathogen effectors to interfere with early PRR signaling (Tang *et al.*, 2017; Zipfel, 2009). The 'Signaling mechanisms' subtopic comprises eight publications. Four publications describe downstream molecular events with: two summarize the complex network of signaling pathways occurring during PTI with an emphasis on mitogen-activated protein kinases (MAPK) and effectors employed to suppress it (Bigeard *et al.*, 2015; Meng and Zhang, 2013); and two highlight the activity of MAPK4 (Qiu *et al.*, 2008) and BIK1 (Lu *et al.*, 2010) in the early signaling pathways and effectors associated with that process. On another hand, two publications study the contribution of phytohormones to the effector recognition (Tsuda and Katagiri, 2010; Yang *et al.*, 2019), one addresses the role of reactive oxygen species (ROS) in signaling and defense reactions against filamentous fungi and fungal effectors that suppress the host oxidative burst (Heller and Tudzynski, 2011), and one provides evidence of calcium-dependent PAMP-triggered immunity in plants (Tian *et al.*, 2019).

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