A Meta-analysis of the known Global Distribution and Host Range of the *Ralstonia* Species Complex

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Abstract

The *Ralstonia* species complex is a group of genetically diverse plant wilt pathogens. Our goal is to create a database that contains the reported global distribution and host range of *Ralstonia* clades (e.g. phylotypes and sequevars). In this fifth release, we have cataloged information from 304 sources that report one or more *Ralstonia* strains isolated from 107 geographic regions. Metadata for nearly 10,000 strains are available as a supplemental table. The aggregated data suggest that the pandemic brown rot lineage (IIB-1) is the most widely dispersed lineage, and the phylotype I and IIB-4 lineages have the broadest natural host range. Although phylotype III is largely restricted to Africa, one strain collection reports a phylotype III strain isolated from Jamaica in the mid-1900s. In the previous release, we included reported presence of phylotype III strains in Brazil, but closer inspection of those results reveals that the strains were actually phylotype I strains that were mis-identified. Similarly, although phylotype IV is mostly found in East and Southeast Asia, phylotype IV strains are reported to be present in Kenya.

Additionally, we have created an open science resource for phylogenomics of the RSSC. We associated strain metadata (host of isolation, location of isolation, and clade) with almost 700 genomes in a public KBase narrative. Our colleagues can use this narrative to identify the phylogenetic position of newly sequenced strains. We further curate a set of 601 high quality genomes based on low contamination and high completeness by CheckM. Our colleagues can use the curated dataset for comparative genomics studies.

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Introduction

Bacterial pathogens in the *Ralstonia* species complex are xylem pathogens that infect a broad range of agricultural and natural plant hosts. *Ralstonia* strains clog plant xylem vessels, leading plant hosts to wilt [1]. Historically, *Ralstonia* strains were classified based on carbon utilization patterns ("Biovar") and host range ("Race"). However, DNA sequence-based taxonomies more accurately reflect the evolutionary relationships of *Ralstonia* lineages.

Currently, the *Ralstonia solanacearum* species complex (RSSC) is classified into three species: *R. solanacearum*, *R. pseudosolanacearum*, and *R. syzygii*. The separation of *Ralstonia* into three species was first proposed by Remenant *et al.* 2010 [2], formalized by Safni *et al.* 2014 [3], and reinforced by Prior *et al.* 2016 [4]. Strains are also classified into a phylotype system, which overlaps with the species boundaries. All *R. solanacearum* strains are within phylotype II, but phylotype II is divided into IIA, IIB, and IIC groups. *R. pseudosolanacearum* strains are either in phylotype I or phylotype III. *R. syzygii* strains are in phylotype IV. Strains are further sub-classified into sequence variants, or "sequevars", based on the DNA sequence of the conserved *egl* endoglucanase gene. Because *Ralstonia* are known to be naturally competent, we hypothesized that horizontal gene transfer of *egl* could confound sequevar-based phylogenies. We recently use whole genome phylogenetic trees to interrogate the robustness of *egl*-based trees [5]. We found that *egl* trees work well for phylotype II, but *egl* trees are less accurate for phylotype I. Although only a small number of phylotype III and IV genomes were analyzed, the longer branch lengths in phylotype III and IV suggests that sequevars/*egl*-based trees may provide effective estimation of these strains' phylogenetic position. Since the phylotype-sequevar system was first developed and described by Prior and Fegan in 2005 [6], hundreds of papers have used this system to describe the genetic diversity of *Ralstonia* isolates around the world. However, there has not been any public database that aggregates this population genetics information.

The *Ralstonia* community typically states that *Ralstonia* strains infect over 250 plant species in over 50 botanical families. Is that an under-estimation? Our goal is to perform a meta-analysis that documents the known host range and global distribution of each sequevar in the *Ralstonia* species complex. We intend to update this preprint at regular intervals as we populate the database. This pre-print also describes a user-friendly KBase narrative[7] that allows users to place new *Ralstonia* genomes within the phylogenomic context of public genome sequences.

Methods

Article Selection Criteria and Search Strategy:

We prioritized articles that used the phylotype and/or phylotype-sequevar system to characterize strains. We identified these articles by using Google Scholar to find the papers and theses that cite "How complex is the *Ralstonia solanacearum* species complex?" by Fegan and Prior 2005 [6]. To get a better estimate of the diversity of documented hosts for *Ralstonia*, we did a search of the literature using search terms like "weeds", "host range", and older names for the pathogen ("*Pseudomonas solanacearum"* and "*Burkholderia solanacearum"*). Additional search terms included: "*Ralstonia solanacearum"*, "*Ralstonia pseudosolanacearum"*, "*Ralstonia syzygii"*, and "First report". The papers included in this database are referenced in Table 1.

Table 1: List of Papers in this Study

Year Published	References
1971	[11–22]
1976	[23]
1978	[11]
1980	[12]
1984	[13]

1986	[14–24]
1993	[25–36]
1995	[37]
1998	[38–51]
1999	[52–54]
2000	[55]
2001	[56–58]
2002	[59]
2003	[60–62]
2004	[63,64]
2005	[65–68]
2006	[69,70]
2007	[71–81]
2008	[82–88]
2009	[89–97]
2010	[2,98–105]
2011	[106–121]
2012	[122–134]
2013	[135–149]
2014	[3,150–167]
2015	[168–185]
2016	[4,186–195]
2017	[196–212]
2018	[213–226]
2019	[227–235]
2020	[236–256]
2021	[257–267]
2022	[5,268–276]
2023	[277–284]
2024	[285–289]
Pre-prints	[290]

Converting strain metadata into a structured format:

We focused on cataloging information that is relevant to the epidemiology of the *Ralstonia* strains: phylogenetic classification, host of isolation, and geographic location where isolated. Additionally, when listed, we include any NCBI accessions for the genome, *egl* marker genes, or other genes.

For **phylogeny**, we record the phylotype (I-IV), sub-phylotype (for phylotype II, this is the IIA, IIB, or IIC subdivisions), and sequevar (1-71). Several sequevars have been subdivided based on phylogeny and/or ecologically important traits, so we created a “sub-sequevar” column to denote these. This includes multiple subdivisions of sequevar IIB-4 and IV-10 sequevar which includes the “*R. syzygii* subspecies *celebensis*” (causes Blood disease of banana) and a clade of the paraphyletic “*R. syzygii* subspecies *indonesiensis*”.

For **host**, we created several columns to annotate the host at multiple taxonomic scales (order to species). We attempted to systematize all common names and species to a unified label. For example, all potato isolates are listed as "Solanum tuberosum (Potato)". The systematic structure will make it easier to use R, python Pandas, or Excel equations to summarize and visualize the contents of the database.

For **location**, we record the most precise location information available (e.g. city, province, or country). We also have columns that describe the location at the country (or territory if the land region is geographically separated from the governing body), subcontinent, and continent levels. Special consideration was applied to reports of strains that were detected on internationally traded plants, such as the detection of IIB-1 strains on greenhouse propagated geranium plants imported into the U.S. [81,255]. For these situations, we included "(imported)" in the location data.

We did not include the Race or Biovar information in the database. For critique of these outdated Race and Biovar classification schemes, see Sharma *et al*. 2022 [5].

Curation, quality control, and correction of strain metadata

Quality control and correction of strain metadata was performed using OpenRefine software and manually in excel. OpenRefine is an open-source data management tool that allows changes to be made across whole columns and datasets. OpenRefine includes many baseline functions that fix common entry mistakes by transforming data *en masse*. The most useful functions for correcting the *Ralstonia* strain metadata include "trim leading and trailing whitespaces," "collapse consecutive whitespace," and "cluster and edit." We used the "cluster and edit" function paired with the "facet" function to group together and perform mass edits on similar strings of characters that were qualitatively the same, such as "Solanum tuberosum", "Solanum tuberosum (Potato)", and "Potato." Using this method, we consolidated values across all metadata. Unfortunately, OpenRefine failed to parse many non-ASCII characters (such as ç, ô, ñ, é, etc.), and automatically replaced these characters with other symbols (such as @&%). Thus, we manually corrected location and host strain metadata in Excel. Missing host taxonomic data was expanded from species name to include genus, family, and order. Location data was similarly expanded to include country, subcontinent, and continent.

Database:

The full dataset is available as a Table S1 with this preprint.

Table 2: Summary of the database versions

Database Release Date	# Papers	Paper published range	# Strains	# Sequevars[b]	# Countries or Territories	# Host plants
2020/07/03	35	2017-2020	1625	57	50	56
2021/03/23	73	2012-2020	3395	over 64[a]	86	124
2021/11/03	93	2007-2020	4924	Over 71	86	139
2022/08/30	197	1971-2022	7794	68[b]	105	392
2024/10/31	304	1971-2024	9931	68[b]	107	504

[a]*As of this release, we have not investigated the sequevar assignment of strains classified into "unknown" or "new" sequevars.*

[B] *Note that sequevar is an imperfect phylogenetic system for phylotype I. See Sharma et al. 2022 for details* [5]

Extracting metadata for genomes available on NCBI.

Genomes on NCBI do not always have a corresponding Genome Announcement or other publication, but most of these genomes are deposited with ecological metadata on the corresponding "BioSample" page. Historically, NCBI taxonomy has been disorganized because of taxonomic revisions in this group. For example, many genomes for "*Ralstonia pseudosolanacearum*" (taxonomy ID: 1310165) and "*Ralstonia syzygii*" (taxonomy ID: 28097) were deposited as "*Ralstonia solanacearum*" (taxonomy ID: 305), primarily because they were deposited prior to the renaming in 2014. Moreover, several genomes of the blood disease pathogen (*Ralstonia syzygii* subsp. *celebensis*) were deposited with their own taxonomy ID due to a peculiar taxonomic rule: these strains could not be formally named because the type strain was not viable in culture collections.

We extracted metadata for all RSSC genomes that we could identify in relevant "taxonomy IDs". For each genome, we listed the "RefSeq Assembly Accession" when possible (GCF_xxx). Some assemblies have been excluded from RefSeq due to problems like "too many frameshifted proteins" or "highly fragmented genome". In this case, we list the GenBank Assembly Accession (GCA_xxx). Unfortunately, while conducting newly implemented quality analyses the NCBI RefSeq staff suppressed the RefSeq genomes for all phylotype I, III, and IV strains that had been uploaded in the species "*Ralstonia solanacearum*" for the reason these genomes were "unverified source organism". Thus, many of RefSeq genomes have been suppressed despite the genome being high quality and, sometimes, complete. As of summer 2024, NCBI has developed automated pipelines to check and report useful information on the new "NCBI Datasets" page: (1) assembly completeness/contamination with CheckM and (2) taxonomic assignment based on ANI to type strains.

Importing genomes into the "RSSC Phylogenomics" narrative on KBase.

KBase is a user-friendly graphical user interface for biological informatics that is developed and maintained with significant investment from the US Department of Energy [291]. Because RSSC genomes are dispersed across several (often inaccurate) taxid pages, we developed a KBase Narrative that can help us and other scientists identify the phylogenetic identity of new RSSC genomes.

We used the structured data on our spreadsheet to assign a systematic name to each genome, such as: "IIC-7_UW853_UCD541_Tomato-Solanaceae_UnitedStates_GCA_036543205.1". The systematic name lists:

1. Phylogenetic information (phylotype, sequevar, sub-sequevar)
2. Strain name (spaces and parentheses removed. Colons and hyphens were often removed, but underscores were often kept)
3. Host of isolation (common name and family)
4. Location (country/territory level)
5. Genome accession

Initially, there were genomes that lacked precise phylogenetic information. To identify the phylogenetic identity of these genomes, we used the KBase App "Batch Create GenomeSet v1.2.0" to create a GenomeSet object that included all genomes in the narrative. Then we used the "Insert Set of Genomes into SpeciesTree v2.2.0" to create a low-resolution phylogenetic tree. This app uses FastTree2 [291] with the -fastest setting to construct a tree based on an MSA of 49 universal bacterial genes. We inspected the tree, and we were able to assign many genomes to phylotypes and sequevars.

Wherever possible, we use the NCBI RefSeq or NCBI Genbank version of the genomes. However, when only the raw reads were available on SRA, we carried out a pipeline of importing the reads from SRA, assessing read quality with FastQC, trimming reads with Trimmomatic (Illumina) with settings to trim adapters when necessary or Filtlong (Nanopore when Illumina short reads were present), assessing trimmed reads with FastQC, assembling with SPAdes (Illumina) or UniCycler (Nanopore and Illumina), and annotation with Prokka.

Results and Discussion

We compiled 9931 strains from over 300 sources. These strains represent over 65 sequevars isolated from 107 countries or territories (Table 2). Most of the reported strains are phylotype I or II strains (Fig. 1). The full dataset is included as Table S1, which is accessible on this pre-print. For each strain, we recorded taxonomy (phylotype and sequevar), host (specific name and the host plant's taxonomic Family and Order), isolation year, isolation location, NCBI accessions (genome or partial sequences of *egl, mutS* and/or *rplB* market genes genes) and the citation. We analyzed some of the host range and biogeographic distributions of the RSSC and phylotypes.

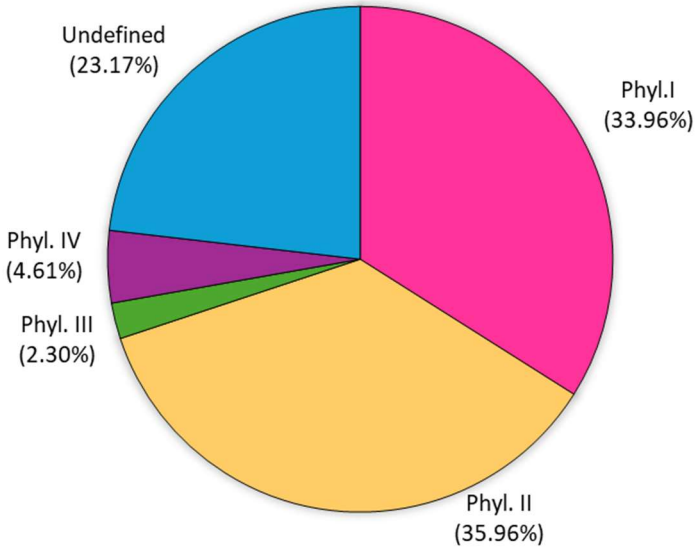

Fig 1. Phylotype assignments for strains in the Global Ralstonia Diversity database (version 2024).

Host Range:

Tables 3-5 summarize information about host range in the RSSC and the phylotypes. Table 6 attempts to look at host range within more narrow clades.

Table 3: The number of unique plant hosts (reported at various taxonomic levels)

	Species	Genus	Family	Order
All RSSC	504	277	86	35
Phyl. I	125	81	43	26
Phyl. II	82	53	36	25
Phyl. III	16	7	5	5
Phyl. IV	20	8	6	6

Table 4: The top 20 most common host species to be listed in the database, sorted by frequency

Host Species	Frequency Reported	% of Total Host Reported
Solanum tuberosum (Potato)	2977	30.91
Solanum lycopersicum (Tomato)	2026	21.04
Capsicum annuum (Pepper)	564	5.86
Solanum melongena (Eggplant)	540	5.61
Musa acuminata (Banana)	437	4.54
Nicotiana tabacum (Tobacco)	344	3.57
Zingiber officinale (Ginger)	220	2.28
Eucalyptus pellita (Large-fruited Red Mahogany)	170	1.77
Anthurium sp. (Laceleaf)	124	1.29
Musa acuminata x balbisiana AAB	119	1.24
Arachis hypogaea (Peanut)	99	1.03
Solanum macrocarpon (African Eggplant)	95	0.99
Pelargonium sp. (Geranium)	92	0.96
Musa paradisiaca (Plantain)	90	0.93
Solanum aethiopicum (Bitter Tomato)	66	0.69
Musa sp. (Banana Plant)	63	0.65
Epipremnum aureum (Pothos)	57	0.59
Solanum dulcamara (Bittersweet Nightshade)	56	0.58
Syzygium aromaticum (Clove)	43	0.45
Eucalyptus sp. (Eucalyptus)	43	0.45

Table 5: Heatmap that attempts to answer the question: "If I have a wilted [plant species], what phylotype is most commonly the culprit? The heatmap is applied to each row.

Host Species	I	II	III	IV
Solanum tuberosum (Potato)	389	1910	104	159
Solanum lycopersicum (Tomato)	1021	527	55	31
Capsicum annuum (Pepper)	368	27	7	2
Solanum melongena (Eggplant)	404	32	9	0
Musa acuminata (Banana)	3	255	0	80
Nicotiana tabacum (Tobacco)	242	34	6	1
Zingiber officinale (Ginger)	143	5	0	0
Eucalyptus pellita (Large-fruited Red Mahogany)	52	110	0	0
Anthurium sp. (Laceleaf)	11	96	0	0
Musa acuminata x balbisiana AAB	0	1	0	118
Arachis hypogaea (Peanut)	59	4	0	0
Solanum macrocarpon (African Eggplant)	89	0	5	0
Pelargonium sp. (Geranium)	10	32	11	0
Musa paradisiaca (Plantain)	1	79	0	1
Solanum aethiopicum (Bitter Tomato)	60	6	0	0
Musa sp. (Banana Plant)	1	39	0	6
Epipremnum aureum (Pothos)	0	18	0	0
Solanum dulcamara (Bittersweet Nightshade)	0	53	0	0
Syzygium aromaticum (Clove)	1	2	0	36
Eucalyptus sp. (Eucalyptus)	0	0	0	0

We investigated which clades of *Ralstonia* have been isolated from the most plant species. When possible, we analyzed distribution at the sequevar level. However, several of the sequevars within phylotype I are polyphyletic [5], so we investigated phylotype I's distribution in aggregate. Results are in Table 6. As a significant caveat, *Ralstonia* host range can vary between strains that are closely related (i.e. between strains in the same sequevar) [73,183,258,269]. Nevertheless, host range patterns often correlate with phylogeny [183,269]. Collectively, phylotype I has a wide host range (125 plant species in 43 botanical families). Phylotype IIB-4 has the next broadest host range (43 species in 21 botanical families). Phylotype IIB-1 has been isolated from 22 plant species in 9 botanical families. However, IIB-1 is also the most widely dispersed lineage, reported in 61 countries, so it has appeared in more population survey studies than other lineages. The IIB-1 lineage is most commonly isolated from Solanaceae and Geranium family plants.

Table 6: RSSC clades whose members have been isolated from the most diverse plants.

Clade	Unique Hosts
I	125
IIA-6	6
IIA-35	7
IIA-38	7
IIA-41	7
IIA-50	7
IIB-1	22
IIB-3	9
IIB-4	43
IIB-54	9
IIB-56	7
IIC-7	8
III-19	6
IV-10	11

Biogeography

Ralstonia strains have been isolated from 107 countries (Fig. 2). Tables 7-8 summarize information about biogeography of the RSSC and the phylotypes. Table 9 attempts to look at distribution of more narrow clades.

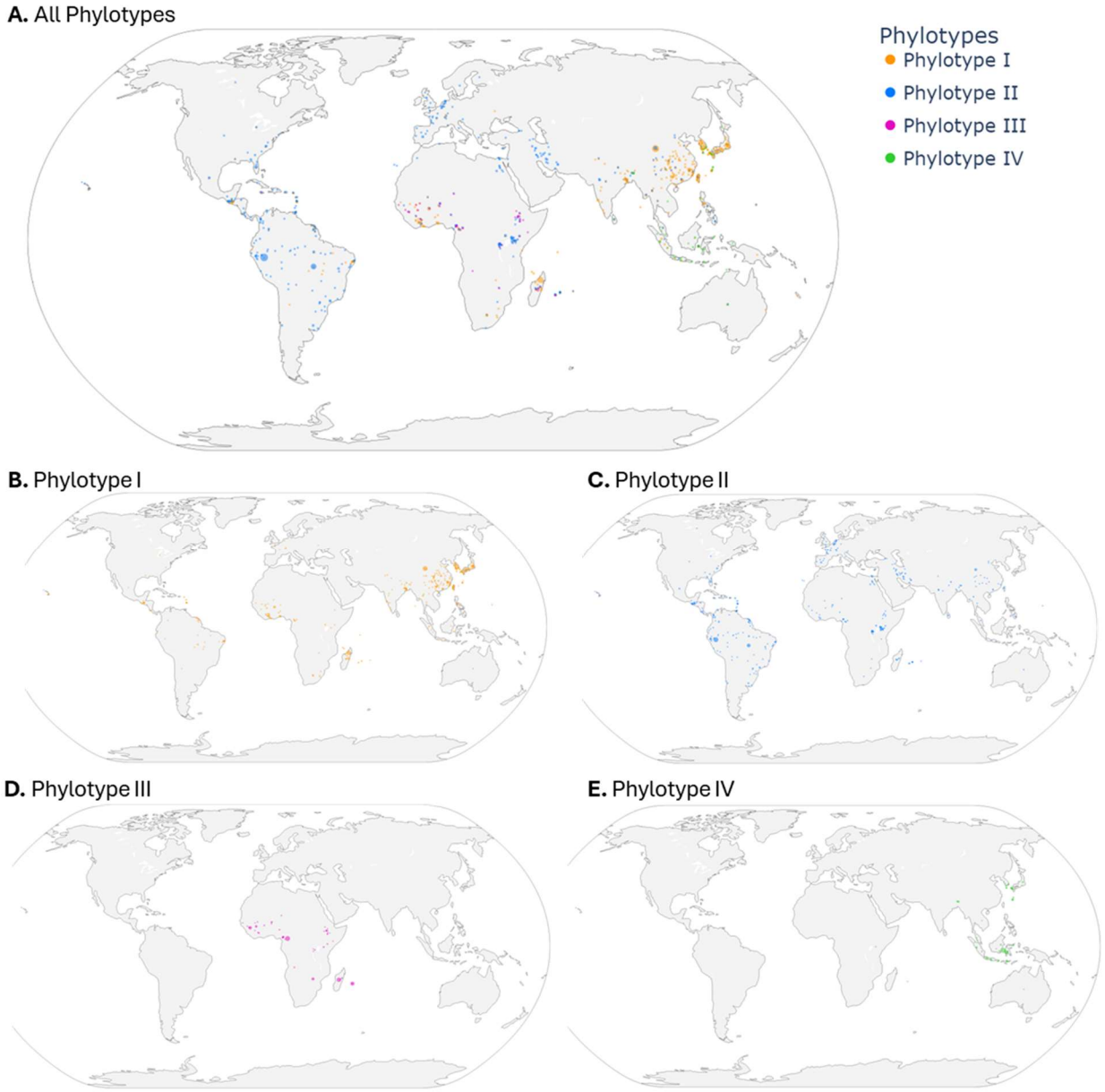

Fig. 2. Locations of strains included in the Global Ralstonia Database. Proportional circles reflect the number of strains reported at that location.

Table 7: Relative distribution of the RSSC and each phylotype, based on the number of unique countries where the strain has been isolated

	Unique Countries
All RSSC	107
Phyl. I	56
Phyl. II	78
Phyl. III	19
Phyl. IV	11

Table 8: Distribution of each phylotype level on different subcontinents. Pink boxes indicate distributions that were unexpected.

	I	II	III	IV
Northern America	x	x		
Central America	x	x		
Southern America	x	x		
Caribbean	x	x	x	
Northern Europe		x		
Central Europe	x	x		
Western Europe	x	x		
Southern Europe		x		
Northern Africa		x		
Western Africa	x	x	x	
Middle Africa	x	x	x	
Eastern Africa	x	x	x	x
Southern Africa	x	x	x	
Western Asia	x	x		
Southern Asia	x	x		x
Eastern Asia	x	x		x
South-Eastern Asia	x	x		x
Micronesia	x			
Melanesia	x			
Australia and New Zealand	x	x		x
Polynesia	x	x		

Invasive Clades

We investigated which clades of *Ralstonia* have been isolated from many countries. When possible, we analyzed distribution at the sequevar level. However, several of the sequevars within phylotype I are polyphyletic [5], so we investigated phylotype I's distribution in aggregate. Results are in Table 9 and Table S1. Although phylotype I has a wide distribution (56 countries), the clonal pandemic brown rot lineage (IIB-1) has been reported in more countries (61 countries). The next most widely dispersed clades are IIB-4, IIA-6, IIC-7, IIA-35, and IIB-3. Many of the widely dispersed clades are known to infect crops (potato, banana, ginger) or ornamentals that are propagated vegetatively.

Table 9: Distribution of clades of *Ralstonia.* Note that each clade below circumscribes different levels of genetic diversity.

Clade	Unique Countries
I	56
IIA-6	11
IIA-35	8
IIA-38	6
IIB-1	61
IIB-3	7
IIB-4	12
IIC-7	10
III-20	4
IV-10	4

RSSC Phylogenomics narrative on KBase

We created an open KBase narrative that has 676 genomes labeled with a structured name that indicates their phylogenetic identity, strain name, host of isolation, subcontinent of isolation, and an NCBI accession number. Because many *Ralstonia* isolates have been shared amongst scientists, either directly or via deposition into strain collections, there are cases where multiple assemblies are available for the same strain. In cases where this is obvious (strain share the same name and overlapping metadata), we selected the best assembly based on CheckM

contamination/completeness. When those values were identical, we selected the genome with the best N50 or fewest contigs.

Version 2 of the Ralstonia Phylogenomics narrative is located at a new location because we decided to update the syntax of the genome names and because the prior narrative was slow to load and run. The prior narrative is listed in version 4 of this BioRxiv pre-print.

- Narrative with 676 public genomes: https://narrative.kbase.us/narrative/189849

Fig. 3 shows a phylogenetic tree of the 676 public genomes available in the KBase narrative. With a free KBase account, anyone can create a copy of these narratives, upload their own assembly to KBase, annotate the genes, and re-build the 49 gene phylogenetic tree to identify the position of new genomes. We will continue to update the narrative as we add genomes, so our colleagues should create a copy of the latest version of the narrative to assess new genomes.

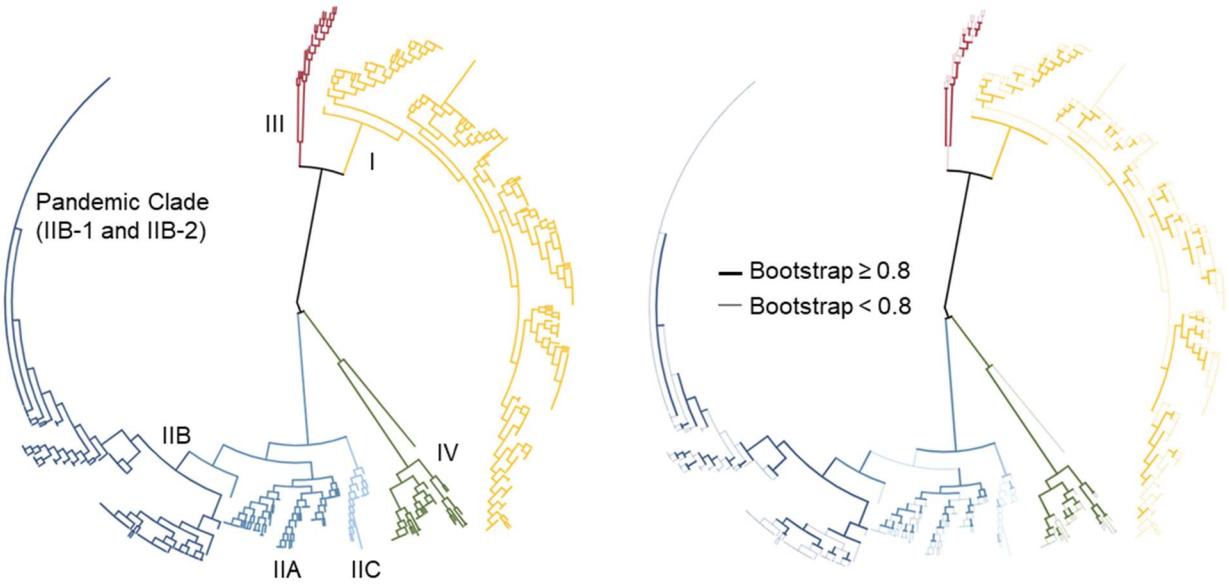

Fig 3. A species tree of 676 RSSC strains with publicly available genomes. The species tree was generated in KBase with the "Insert Set of Genomes Into SpeciesTree - v2.2.0" app, which creates an approximately maximum likelihood tree with FastTree2 based on 49 conserved bacterial genes. To create the stylized tree, the Newick tree file was visualized in iTol [292]. A PDF and .Newick version of the tree are available in the Supplemental Data. The PDF has each genome labeled in searchable text. Phylotype III (n=17), I (n=280), IV (n=38), IIC (n=19), IIA (n=66), IIB (n=256), IIB-1 (n=150).

Fig. 4 shows the RSSC species tree with annotations for the host plant for each strain. These figures and any correlation between *Ralstonia* genomes and host-of-isolation should be interpreted with a grain of salt. Importantly, *Ralstonia* strains are generalist pathogens with complex patterns of host range. The phylogenetic patterns of host-of-isolation reflect scientist's choices (e.g., which plants to survey, which strains to sequence genomes, etc.) in addition to biology (e.g., many Solanaceae are susceptible to diverse *Ralstonia*, phylotype I causes most infections of Zingiberaceae, etc.).

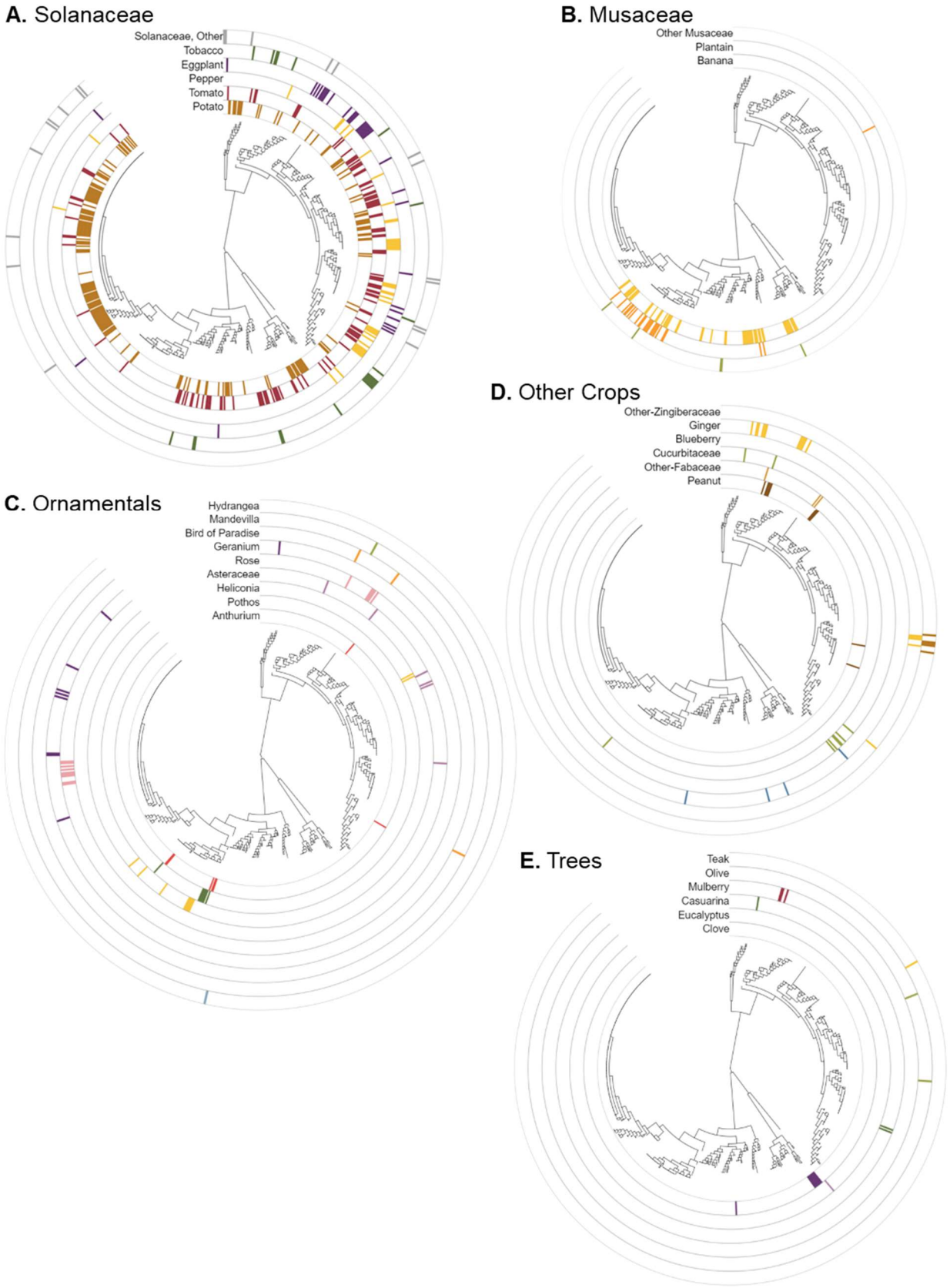

Fig 4. The hosts of isolation RSSC strains with publicly available genomes. The species tree is from Figure 3 and the tree was annotated in iTol.

Assessing quality of genomes for downstream analyses

Not all genome assemblies are equal. Assemblies can suffer from many flaws. We did not import genomes that NCBI flagged as "many frameshifted proteins" (often due to being a Nanopore-only assembly) or "fragmented assembly" (4700+ contigs, which suggests that the user uploaded only the coding sequences instead of the actual assembly).

For the assemblies imported into the KBase narrative, we used CheckM to assess their quality. CheckM yields estimates of the genomes' completeness (are all of the expected single-copy genes present in the genome assembly?) and contamination (are there multiple homologs of the expected single-copy genes, suggesting that an unrelated genome has contaminated the assembly?). For completeness, we set a cut-off of requiring genomes to have no more than 4 missing "single copy genes". This generally corresponds to a 99% complete cut-off. For contamination, we set a cut-off of 1%.

Based on CheckM analysis, we classified 83 genomes as low-quality (24 genomes for low completeness and 51 genomes for high contamination, and 8 genomes that yielded errors with CheckM). For example, all of the draft genomes from Ailloud et al. 2015 have low completeness, likely because they were assembled from very short Illumina reads (2 × 50-bp) due to the technology available at the time. The Ailloud et al. 2015 genomes are estimated at 96-98% complete, which means the assemblies could be missing upwards of 200 genes. Two additional genomes have very low completeness: phyl. IIA-38 genome P816 was 81% complete and phyl. I genome VT0801 is 91% complete. Fig. 5 shows which genomes were included in the high quality genome set.

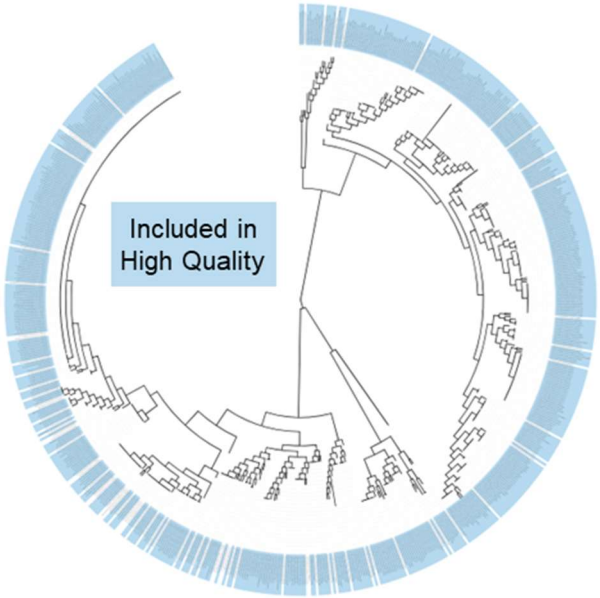

Fig 5. Phylogenetic distribution of high and low quality RSSC genomes. The species tree is from Figure 3 and the tree was annotated in iTol. Genomes with high CheckM completeness and low CheckM contamination are annotated in blue.

Conclusion

Bacterial wilt pathogens in the *Ralstonia* species complex are high impact global pathogens. We created a strain database that we will regularly update to document the distribution and host range of *Ralstonia*.

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