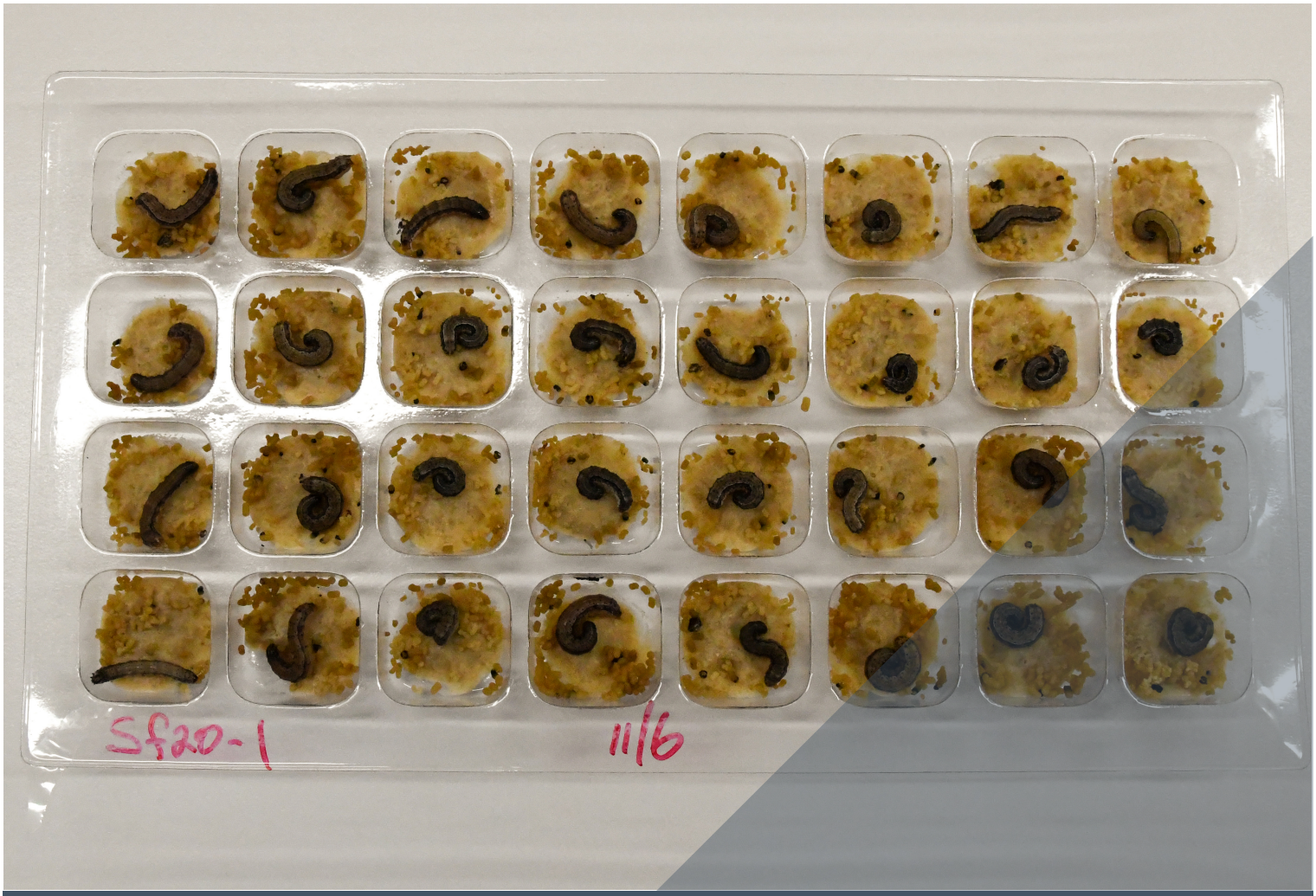

Genomic insights of FAW movement in Australia

Final Technical Report

April 2023

Plant Health AUSTRALIA

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Genomic insight of FAW movement in Australia

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Contents

1 SUMMARY

This study seeks to generate further details and to elucidate pathways of incursion and patterns of population genome diversity and dynamics of the invasive fall armyworm (FAW) *Spodoptera frugiperda* within Australia's agricultural landscape, following its successful establishment as a novel invasive global pest species since January 2020. While the project was impacted by the COVID-19 pandemic especially with respect to sourcing FAW populations from both within Australia (e.g., from Western Australia), and from international collaborators (e.g., Thailand, Indonesia, Cambodia, Solomon Islands, Norfolk Island), samples obtained from Northern Territory and the eastern states of Australia (Queensland, New South Wales, and Victoria), as well as from New Zealand nevertheless provided novel insights on pest population movements and highlighted anthropogenic impact across both spatial and temporal scales.

Highlights from this project included:

- A comprehensive population genomic survey of northern and eastern FAW populations in Australia
- The first genomic analysis of New Zealand invasive FAW individuals
- Evidence of high genetic diversity in Australia FAW population through detection of high numbers of C-strain and R-strain mitochondrial genome haplotypes
- Expected patterns of admixture homogenisation were not observed in recent Australia (i.e., AUS_22) populations; instead, unexplained clusters in some populations from NSW, QLD and WA were detected.
- Genetic differentiation analyses identified substructure within Australian populations, whereby QLD populations were more similar to NT populations, than neighbouring populations
- Genomic evidence of bridge-head populations in Asia/Southeast Asia that were focal points of FAW population movement towards Australia/New Zealand.
- Dynamic and fluid population composition, unexplained by natural processes such as drift and adaptation
- Identifying gaps in regional biosecurity, leading to multiple anthropogenically derived introgressions into Australia, and therefore highlighting a need for future studies that consider regional genetic diversity
- More selection analyses are required to understand the impact of regional genetic diversity on genes of biosecurity importance, e.g., are there FAW populations exhibiting evidence of harbouring genes with detrimental effects?

2 Background

The highly polyphagous agricultural New World lepidopteran pest *Spodoptera frugiperda* (fall armyworm, FAW) had undergone range expansion across the Old World regions (Africa, Asia, Oceania) in recent years. International scientific and agricultural communities, plant health protection organizations, and government agencies have largely accepted the axiom of the pest's 'west-to-east' spread due to its chronological order of reporting since officially detected in western Africa in 2016 (Goergen et al., 2016). Acceptance of the west-to-east spread of FAW across the Old World implies also accepting that this spread originated from West Africa, and that the founding population carried limited genetic diversity as detected based on single gene markers such as based on partial mitochondrial DNA (e.g., cytochrome oxidase subunit I (mt*COI*); cytochrome B (cyt *b*), cytochrome oxidase subunit III (mt*COIII*) genes (Cock et al., 2017; Nagoshi et al., 2018; Otim et al., 2018) and/or partial Triose Phosphate Isomerase (*TPI*) nuclear gene (Nagoshi, 2010; Nagoshi et al., 2019b). Genomic surveys (Rane et al., 2022a; Schlum et al., 2021; Tay et al., 2021b; Tay et al., 2022d) however, supported multi-directional introductions and significant genetic diversity in various invasive FAW populations from Africa and Asia (India, China) analysed, as reflected also from bioassay experiments and resistance gene characterisation (e.g., Boaventura et al., 2020; Deshmukh et al., 2020; Eriksson, 2019; Guan et al., 2021; Lv et al., 2021; Tay et al., 2021a; Tay et al., 2022c; Yainna et al., 2021).

Disentangling between single vs. multi-directional spread of the FAW has significant implications on implementation and adoption of guidelines and policies necessary to protect plant health and agricultural productivity. The importance of attributing the correct incursion and spread pathways for the FAW based on well-supported science-based evidence are of two folds, acceptance of a 'west-to-east' spread could therefore: (i) result in on-going and/or future incursions in affected countries not being realised, and could lead to introductions of new genetic traits that could negatively impact agricultural and horticultural output, and (ii) limit the understanding and expectation of global pest introduction pathway complexities, thereby impeding global efforts to protect plant health due to increasing risks of introducing novel plant pests and diseases.

In Australia, the FAW was officially reported from Bamaga, northern Queensland, on 31-January 2020, followed by rapid detections also in Strathmore, Queensland, on 19-February 2020, and in Western Australia (WA) in March 2020. Since this initial stage of detections, this pest has progressively been reported southward along the eastern and western coastal regions, extending as far south as Victoria and Tasmania, including Norfolk Island in the Pacific, leaving South Australia as the only mainland Australian state currently not yet affected by this pest. Reverse trajectory study (Qi et al., 2021) as well as based on simple untested assumption (Wan et al., 2021) have suggested that the current Australian FAW populations involved a single pathway into Australia and originated from a single population source from Indonesia. With this simplistic assumption of a single introduction and founder event, the FAW populations in Australia would therefore reasonably be expected to harbour limited genomic diversity, and would also exhibit widespread genome harmonization between populations.

Population genome surveys of the initial FAW populations in Australia from Western Australia (WA), Northern Territory (NT), Queensland (Qld), and New South Wales (NSW), representing generations from the first year since FAW's arrival in Australia, identified distinct genomic signatures between Australian populations (Rane et al., 2022a; Tay et al., 2022b; Tay et al., 2021b), supported also by bioassay studies involving WA and Qld populations (Tay et al., 2021a; Tay et al., 2022b; Tay et al., 2022c), and suggested multiple introduction pathways from Southeast Asia (SEA) into Australia, as well as establishment of genetically distinct and diverse FAW populations in Asia/SEA. The genome databases of Tay et al. (2022d) and Rane et al. (2022a; b; c) of populations from the Far East (i.e., South Korea), SEA (i.e., Malaysia, Philippines, Vietnam, Laos, Myanmar), Pacific (i.e., Papua New Guinea (PNG))/Oceania (i.e., Australia), Asia (China, India), Africa (Uganda, Malawi, Benin, Tanzania), and from the pest's native ranges (Brazil, Peru, Mexico, French Guiana, Guadeloupe, Puerto Rico, Florida, Mississippi) represent valuable resources to help address priority knowledge gap of: (i) how on-going natural migration events from Asia/SEA regions impact

on the genetic diversity of established FAW populations in Australia, and (ii) what are the patterns of population movements within Australia at both spatial and temporal scales?

2.1 Objectives

The objectives of this study are of two folds:

(1) to apply established population genomic analysis pipeline to understand the genetic contributions of new migrants to the established Australia FAW populations, and

(2) to understand the level of population connectedness between FAW populations in Australia.

3 METHODS

3.1 Samples

We sourced additional Australia FAW populations from WA, NT, QLD, NSW, and Victoria (VIC) to infer population gene flow patterns and connectivity using population and evolutionary genomic approaches. We also incorporated population genomic data established by Tay et al. (2022d) and by Rane et al. (Rane et al., 2022a; b; c) (and where possible, incorporated also other published whole genome sequencing data involving various native and invasive range FAW populations) to assist with achieving the project objectives. Currently whole genome sequencing dataset for invasive FAW populations have been report from China, Africa, (Guan et al., 2021; Gui et al., 2020; Schlum et al., 2021; Xiao et al., 2020; Zhang et al., 2022) and also the various New World native ranges (e.g., Gui et al., 2020; Schlum et al., 2021). Finally, we will also attempt to seek additional populations representing more recent invasive populations such as from the Pacific and from New Zealand (NZ). The list of new material received for this project are provided in Table 1 below, and their map locations are as shown in Fig. 1.

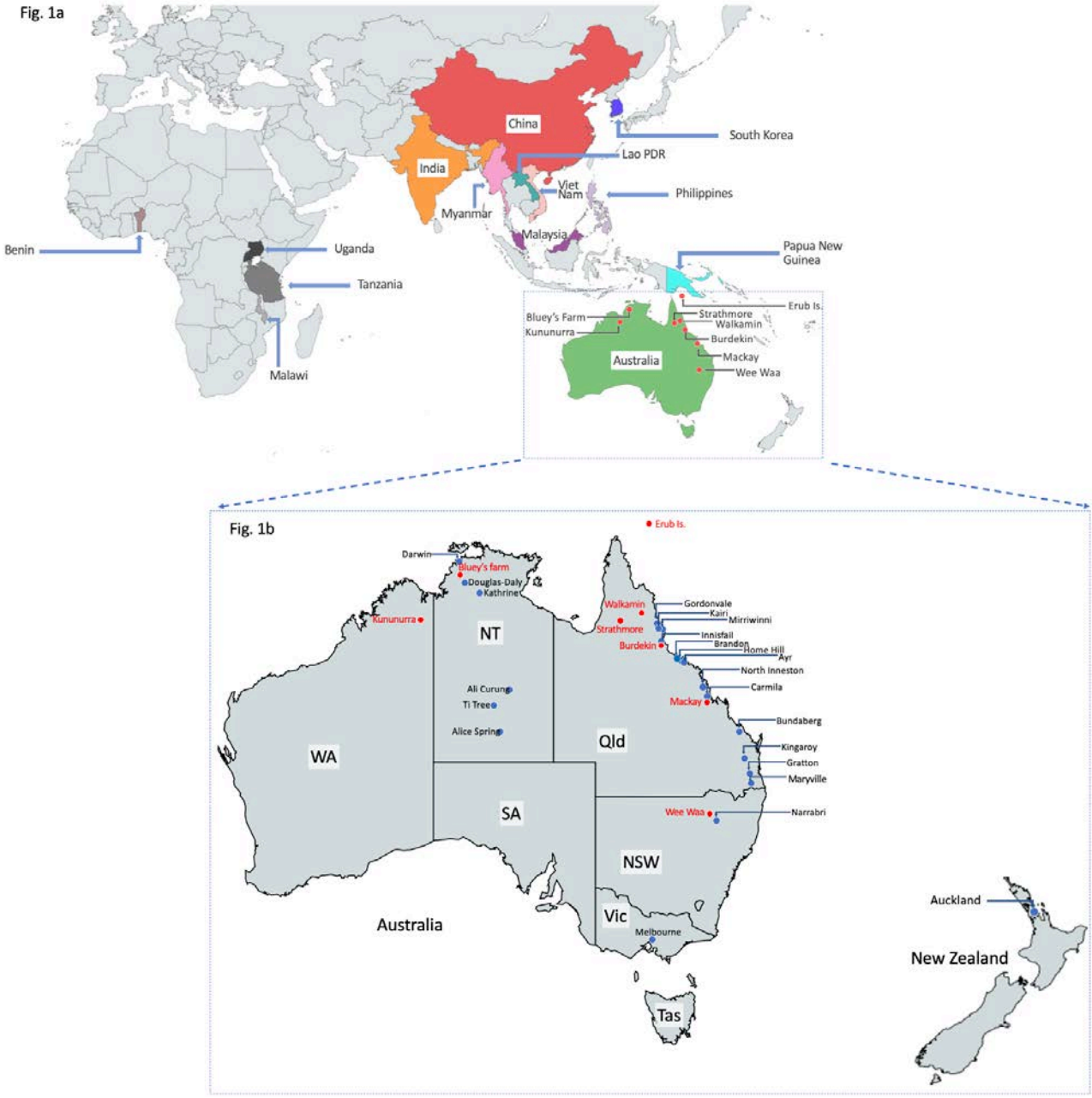
Table 1: *Spodoptera frugiperda* (FAW) populations from Australia and New Zealand used in this project. Australia FAW populations listed here represent 2nd year populations post incursion, and New Zealand population represent the first-year population since its first report in April 2022.

State	Population	Code	Number	Date
New South Wales	Narrabri	FAW-1, 3, …, 10	9	10 Dec 2021
	Narrabri	FAW-11, …, 30	20	17 Dec 2021
	Narrabri	FAW-31, …, 40	10	21 Dec 2021
Queensland	Carmila	FAW-150, …, 154	5	25 Jan 2022
	Gordonvale	FAW-155, …, 159; 178, …181	9	06 Jan 2021
	Mirriwinni	FAW-174	1	13 Jan 2022
	Home Hill	FAW-160, 161, 245, 246	4	22-26 Oct 2021
	Brandon	FAW-240, …, 244	5	22 Oct 2021
		FAW-235, …, 239	5	26 Oct 2021
		FAW-140, 141, 143, 144	4	18 Nov 2021
		FAW-145, …, 149	5	01 Dec 2021
		FAW-247, …, 251	5	07 Dec 2021

	North Inneston	FAW-175-177, 252, …, 258	10	25 Jan 2022
	Innisfail	FAW-162, …, 166, 182, 229-231	9	17 Dec 2021
	Maryville	FAW-167, …, 173, 232	8	09 Dec 2021
	Ayr	FAW-259, …, 263, 265, …, 268	9	13 Apr 2022
	Bundaberg	FAW-269, …, 278	10	01 Mar 2022
	Gatton	FAW-279, 282, …, 287	7	07 Feb 2022
	Kairi	FAW-289, …, 298	10	17 Feb 2022
	Kingaroy	FAW-299, …, 308	10	29 Mar 2022
Victoria	Various	FAW-P315, P317, …, P338	23	15 Sep 2020 – 7 Apr 2022
Northern Territory	Ali Curung	FAW-41, …, 45	5	Jan 2021
		FAW-139, 220, …, 228	10	Mar 2021
		FAW-46, …, 49	4	Sep 2021
		FAW-309, …, 314	6	Sep-Oct 2021
	Alice Spring	FAW-233, 183, …, 186	5	Jan 2021
		FAW-315, …, 322, 185, 186	10	Mar-Apr 2021
		FAW-323, …, 327, 190, 191	7	May-Jun 2021
		FAW-60, …, 64	5	Sep 2021
		FAW-65, 66	2	Oct 2021
	Darwin	FAW-67-69, 192, …, 194	7	Jan 2021
		FAW-72-74, 329	4	Feb 2021
		FAW-196, …, 204, 234	10	Apr 2021
	Douglas-Daly	FAW-205, …, 214	10	Feb 2021
		FAW-76, …, 85	10	Mar 2021
	Kathrine	FAW-86, …, 90	5	Mar 2021
		FAW-91, …, 95	5	Apr 2021
		FAW-96, …, 100	5	Jul 2021
		FAW-215, …, 219	5	Sep 2021
	Ti Tree	FAW-101, …, 106	6	Feb 2021
		FAW-111, …, 115	5	May 2021
		FAW-126-128	3	Sep 2021
		FAW-129, …, 133	5	Oct 2021
		FAW-134, …, 138	5	Nov 2021
New Zealand	Auckland	FAW-P310, …, P313	4	April 2022

Note: A total of 35 FAW samples failed to sequence successfully, likely due to inadequate genomic quality as a result of poor sample preservation. These failed samples were excluded from downstream evolutionary and population genomic analyses.

Fig. 1: FAW populations from invasive ranges included in this study. **(1a)** FAW populations from Tay et al. (2022d) and Rane et al. (2022a). **(1b)** New populations (blue circles) of FAW from Australia (Northern Territory (NT), Queensland (Qld), New South Wales (NSW), Victoria (Vic)) representing 2nd year post incursion, and from New Zealand (NZ) representing 1st detected population. Australia FAW populations in red circles represent year-1 incursion and have been reported and analysed in (Rane et al., 2022a). The map was created from MapChart <https://www.mapchart.net> and modified using PowerPoint for Mac v16.68. Fig. 1a was modified from Rane et al. (2022a) and used with authors' permission.



3.1.1 DNA extraction

DNA extraction and whole genome sequencing for all the 313 samples was carried out following the approach described in Rane et al. (2022a) and Tay et al. (2022d). Sequencing of the samples was carried out at AGRF or Azenta.

3.1.2 Sequence analyses

Genome sequencing data for each individual were pre-processed to remove contaminants using Trim Galore! (v 0.6.6; https://www.bioinformatics.babraham.ac.uk/projects/trim_galore/) and aligned to published *S. frugiperda* rice genome (v1.0) (Gouin et al., 2017) using bwa_mem2 (v2) (Vasimuddin et al., 2019). We used SAMBLASTER (v 0.1.26) (Faust & Hall, 2014) to remove duplicate alignments and SAMtools (v1.9) (Li et al., 2009)) for sorting processed sequence data. Variants were predicted using BBMap (v38.90) (Bushnell, 2014) and normalised using bcftools (1.9) (Li et al., 2009). Variants were subsampled using regions flanking the 870 single nucleotide polymorphisms (SNPs) from Tay et al. (2022d) for further analyses to minimise batch effects.

3.1.3 Confirmation of species identity

Complete mitochondrial DNA genomes (mitogenomes) of all Australia putative *Spodoptera frugiperda* samples representing post 1st year incursion, as well as the candidate 1st year New Zealand FAW individuals from Auckland region were assembled, aligned, and annotated to confirm assembly quality and to identify the 13 protein coding genes (PCGs) vs. RNA genes (22 tRNAs, 2 rRNAs) and the A-T rich region representing the origin of replication. Confirmation of the *S. frugiperda* species status and individual strain identities (i.e., C-strain (previously Corn-preferred) vs. R-strain (previously Rice-preferred); see Tay et al., (2022a)) was through the partial mitochondrial DNA cytochrome oxidase sub-unit I (mt*COI*) gene identity using BLASTN search (Altschul et al., 1990). Confirmed *S. frugiperda* trimmed and concatenated mitogenomes (see below) were categorised into frequencies and identity using FaBOX (Villesen, 2007; Table 2).

3.1.4 Mitogenome phylogenies

All C-strain and all R-strain FAW individuals were separately grouped within Geneious Prime Version 2022.2.2 (Biomatters Ltd., Auckland) and processed separately. All grouped mitogenomes were aligned using MAFF Align (Katoh et al., 2002; Katoh & Standley, 2013) using default parameters (mafft –maxiterate 1000 --localpair) for trimming to remove all RNA genes (22 tRNAs, 2 rRNAs), intergenic, and the A-T rich regions. To infer the mitochondrial genome phylogenies of all C-strain and R-strain FAW, we concatenated all 13 trimmed protein coding genes (PCGs) with partition for phylogenetic inference using IQ-Tree (Minh et al., 2013; Trifinopoulos et al., 2016), with node support estimated using 1,000 UF-Boot replications (Minh et al., 2013).

3.1.5 SNPs selection

To reduce ascertainment bias, the samples were then pruned to remove all samples with >30% missing data and SNP's with less than 20% missing data to create the final SNP set containing 278 individuals and 870 multi-allelic SNP's. All the multiallelic SNPs were used to calculate population statistics using PLINK 2.0 (https://www.cog-genomics.org/plink/2.0/).

3.1.6 Principal Component Analysis

Principal Component Analysis (PCA) was also carried out to increase interpretability of the large and complex FAW genomic dataset through maximising variance by creating new uncorrelated variables and to aid in visualisation. PCA based on the 870 SNPs was performed using PLINK 2.0 and visualised using ggplot2 (Wickham, 2016). The PCA was restricted to samples from Australia and New Zealand to identify any underlying clustering, which might suggest sequential, or independent introductions.

3.1.7 Gene flow analysis

Furthermore, F_{ST} were estimated between pairs of populations using the Hudson correction (Bhatia et al., 2013) to minimise the effect of rare alleles. This was used to compare disparate populations that were more likely to possess unique (i.e., rare) and novel alleles with the same statistical confidence. This correction approach therefore helped to minimise rare-allele effects that could artificially inflate and bias F_{ST} estimates (i.e., between populations with different rare allele compositions) since closely related populations would be less likely to have rare alleles. Due to low sample size in some populations, the F_{ST}'s were corrected to deliver an absolute estimate and account for rare alleles relegating the need for a Chi-Square based significance test.

Admixture analyses were carried out using the 'admixture' package (Alexander et al., 2009) using 595 bi-allelic SNP's (where there were only two possible alleles across all the 727 individuals). The analyses were visualised using the POPHELPER app (https://pophelpershiny.serve.scilifelab.se/) and labels clarified using Microsoft PowerPoint.

4 RESULTS

4.1 Mitochondrial genome analyses

A total of 20 C-strain and 240 R-strain individuals were identified from new Australia and New Zealand samples processed for this project. Full mitochondrial genomes of all current samples showed similar lengths as previously reported in Tay et al. (2022d) and Rane et al. (2022a) with minor nucleotide length variations occurring at the intergenic and the A-T rich regions. Categorisation of trimmed and concatenated PCG sequences (11,195bp) that included previously characterised mitogenomes (Rane et al., 2022a; Tay et al., 2022d) identified a total of 75 and 34 unique C-strain and R-strain mitochondrial genomes, respectively, despite that there were more R-strain individuals detected (n = 240) than there were C-strain individuals (n=20). Interestingly, combining the two partial mt*COI* haplotypes previously reported in the NT FAW populations (i.e., MW454865, MW454866) by Piggott et al. (2021) and the 20 C-strain individuals resulted in three unique partial mt*COI* haplotypes (Fig. 2), with 19 of the 20 C-strain individuals from this study sharing the same partial mt*COI* sequence identity as MW454866. Taken as a whole, full mitogenome characterisation from our study and the partial mt*COI* gene characterisation from Piggott et al. (2021) identified 20 C-strain mitochondrial haplotypes representing 20 C-strain maternal lineages in Australia.

Of the 240 R-strain FAW individuals from Australia and New Zealand that were successfully sequenced (236 Australia, 4 New Zealand; Table 1), there were 23 unique (i.e., not reported by Tay et al. (2022d) and Rane et al. (2022a)) mitogenome haplotypes detected in this study from 128 of the 240 individuals. A total of 112 FAW (n = 103 and n = 9) clustered with two mitogenome haplotypes that were previously reported from other invasive ranges (Africa, Asia, SEA, and Pacific/Australia; see Rane et al. (2022a)).

Fig. 2: Extracted and aligned mitochondrial DNA cytochrome oxidase sub-unit I (mt*COI*) partial gene sequences from 20 C-strain FAW individuals and aligned with the two partial mt*COI* haplotypes (MW454865, MW454866) identified by Piggott et al. (2021). Square red boxes indicate nucleotide changes. A total of three partial mt*COI* gene haplotypes were identified, with the MW454865 haplotype (Piggott et al., 2021) from a Northern Territory (NT) individual being the most divergent. Nucleotide length and positions in base pairs are shown.

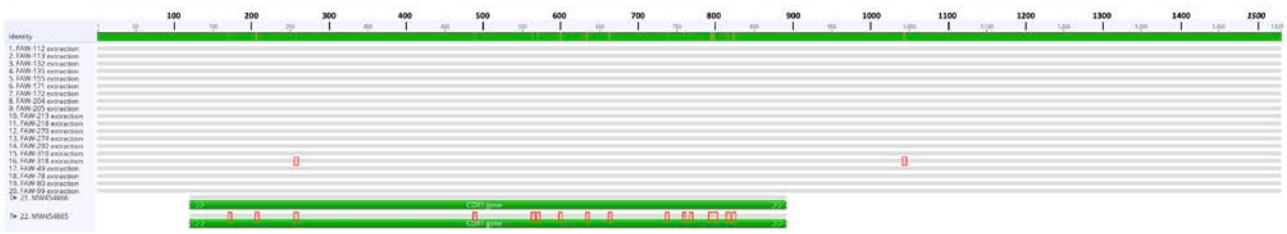


Table 2: Summary of unique C-strain and R-strain *Spodoptera frugiperda* mitogenome haplotypes from 11,195 bp of 13 concatenated protein coding genes (PCGs).

Strain	Haplotype number	Frequency	Note
C-strain	1, 3, 4, 6, 7, 8, 9, 28, 35, 36, 39, 40, 41, 72, 74, 75	1 each	Each haplotype is unique
	2	2	Two individuals in this unique haplotype
	10	1	Included: Malawi, Laos, Philippines, Myanmar, Malaysia, Vietnam
	33	1 (FAW-247)	Included: Malawi, Laos, Philippines, Myanmar, Malaysia, Vietnam, Benin
R-strain	13, 15, 17, 18, 19, 20, 21, 22, 23, 26, 27, 28, 29, 31, 32, 33, 34	1 each	17 unique haplotypes detected in 17 AUS_22 individuals
	12	8	AUS_22 FAW-14, 191, 25, 27, 317, 37, 61, 63)
	14	2	Two AUS_22 individuals (FAW-143, 282)
	16	93	93 AUS_22 individuals
	24	2	Two AUS_22 individuals (FAW-48, 165)
	25	3	Three individuals (FAW-207, 307, 334)
	30	3	Three AUS_22 individuals (FAW-34, 40, 179)
	2	103	Total of 217 samples Included: PNG, Myanmar, Laos, Australia, Vietnam, Philippines, South Korea)
	11	9	1 AUS_21 sample and 9 AUS_22 samples (FAW-19, 22, 84, 106, 157, 181, 208, 219, 312)

Inference of C-strain (Fig. 3) and R-strain (Fig. 4) mitogeneome phylogenies also included previously characterised mitogeneomes from Tay et al. (2022d) and Rane et al. (2022a) to assist with identifying novel haplotypes (i.e., representing previously unrecognised maternal lineages) being detected in this study in Australia FAW populations. While it is tempting to attempt to infer the source populations of Australia invasive FAW based on the C- and R-strain mitogenome phylogenies, it is nevertheless important to keep in mind that the overall low bootstrap support values for majority of branch nodes, largely due to the low number of informative nucleotide sites in the mitogenomes of *S. frugiperda* as a whole.

The concatenated mitogenome phylogenies in Figs. 3 and 4 are therefore best serve to inform of novel haplotypes representing previously unknown maternal lineages in Australia, and which could indicate continued arrivals of novel FAW populations. The report of Tay et al. (2022b; Fig. 2a) that applied a metabarcoding approach for high density landscape-wide FAW-population mt*COI* strain identification surveyed 225 FAW from WA to detect three C-strain individuals (i.e., 1.33%) in the 2020 Kununurra WA populations. Similarly, Piggott et al. (2021) surveyed 45 adult male FAW individuals representing early incursion stage populations (18 March 2020 – 29 April 2020) from NT, and identified the C-strain composition of 4.44% (i.e., 2/45). Rane et al. (2022a) characterised a total of 109 Australia FAW samples between 03 March 2020 to November 2020 and did not detect any C-strain individual. The early-stage C-strain FAW frequencies in Australia therefore appeared low (i.e., 6 C-strain FAW detected from a total of 379 (= 1.58%)). Contrasting these early incursion phase population diversity survey results, the current C-strain detection rate is approximately 5x greater (i.e., ((20/256)x100%)/1.58% = 4.94) in the second year post incursion and with apparent greater C-strain haplotype diversity.

Fig. 3: Concatenated mitogenome phylogeny (11,195 bp) of C-strain *Spodoptera frugiperda* (FAW) detected in this study and in previous studies of Tay et al. (2022d) and Rane et al. (2022a). A total of 20 FAW from this study have the C-strain mitogenomes as indicated by orange branches. Arrows indicate unique mitogenome haplotypes. Arrows within red box are shared haplotypes with multiple individuals. Black branches are C-strain mitogenomes previously reported (Rane et al., 2022a; Tay et al., 2022d). Bootstrap values are shown for 87-100% (red circles) and for 74-86% (grey circles) from 1,000 UF-Boot (Minh et al., 2013).

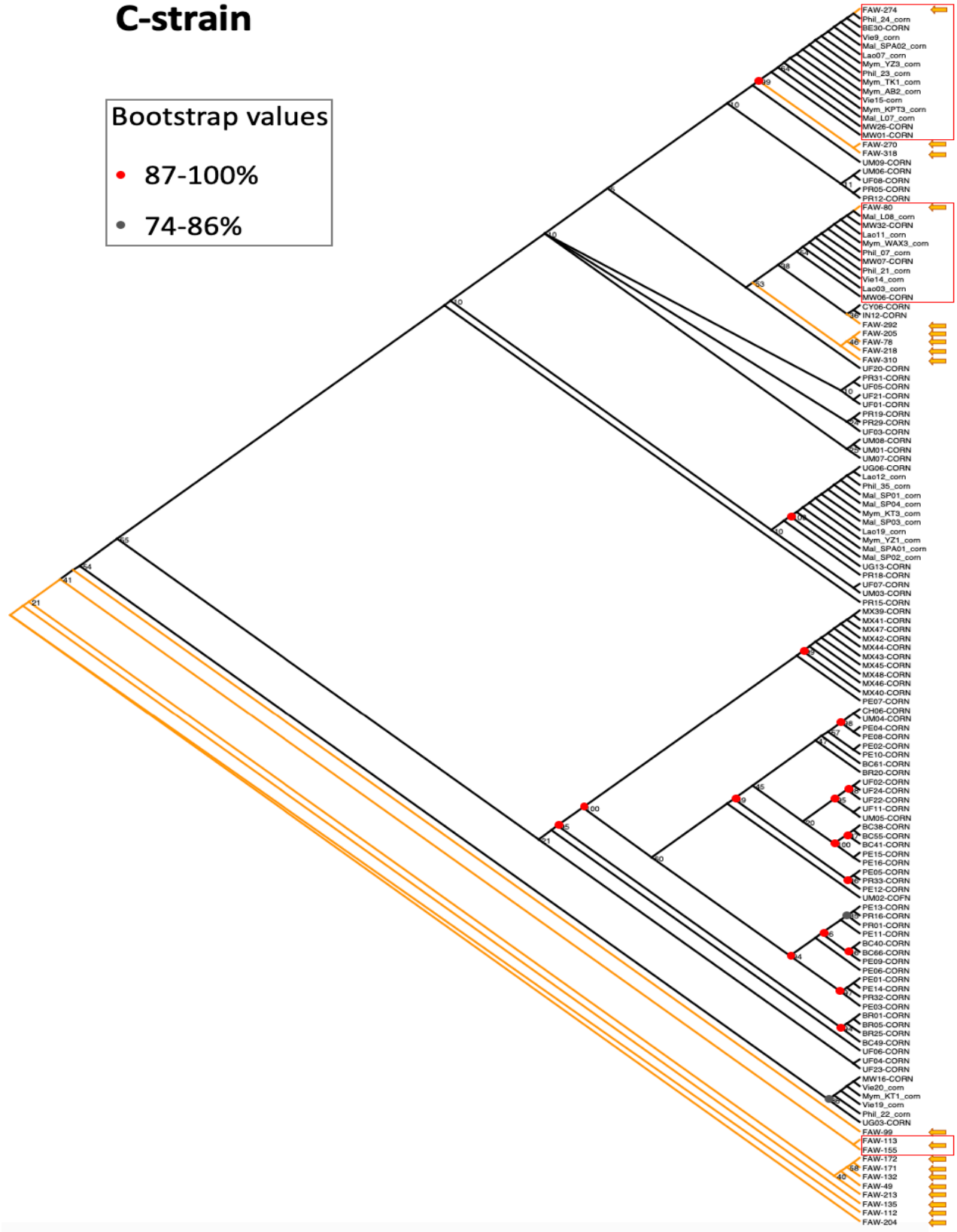
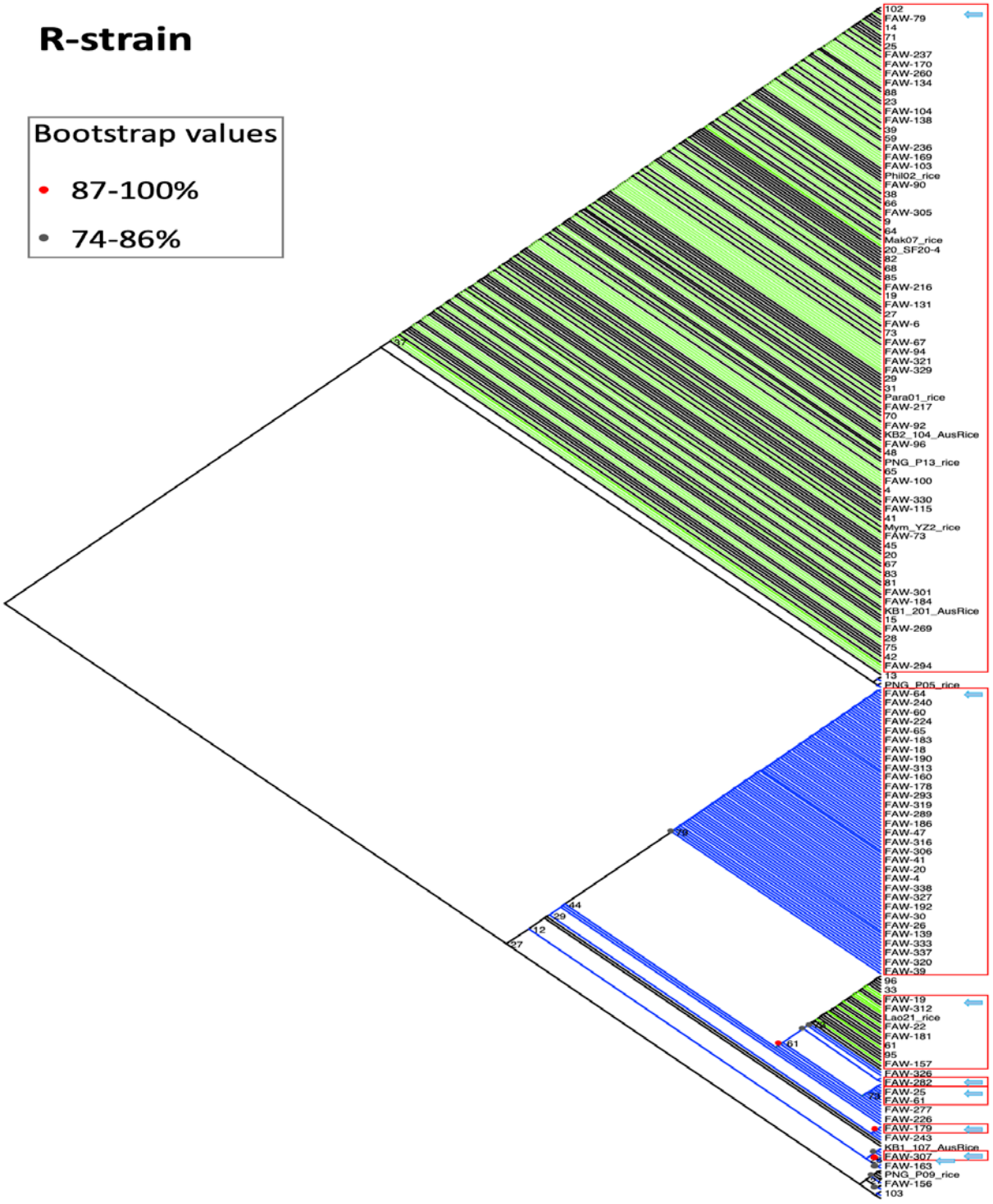


Fig. 4: Concatenated mitogenome phylogeny of R-strain *Spodoptera frugiperda* (FAW) detected in this study and in previous studies of Tay et al. (2022d) and Rane et al. (2022a). A total of 25 mitogenome haplotypes were identified from 240 AUS_22 and 4 New Zealand FAW individuals, of which 23 mitogenome haplotypes were unique (i.e., not detected in the studies of Tay et al. (2022d) and Rane et al. (2022a)). FAW individuals in black branches are R-strain mitogenomes previously reported (Rane et al., 2022a; Tay et al., 2022d), green branches are current Australia and New Zealand FAW individuals that shared mitogenome haplotypes with Asia, Africa, Southeast Asia, Pacific, and Australia FAW individuals that were previously reported in Tay et al. (2022d) and Rane et al. (2022a). Mitogenome haplotypes with multiple (i.e., ≥ 2) FAW individuals are in red boxes. Bootstrap values from 1,000 UF-Boot (Minh et al., 2013) are shown for 87-100% (red circles) and for 74-86% (grey circles).

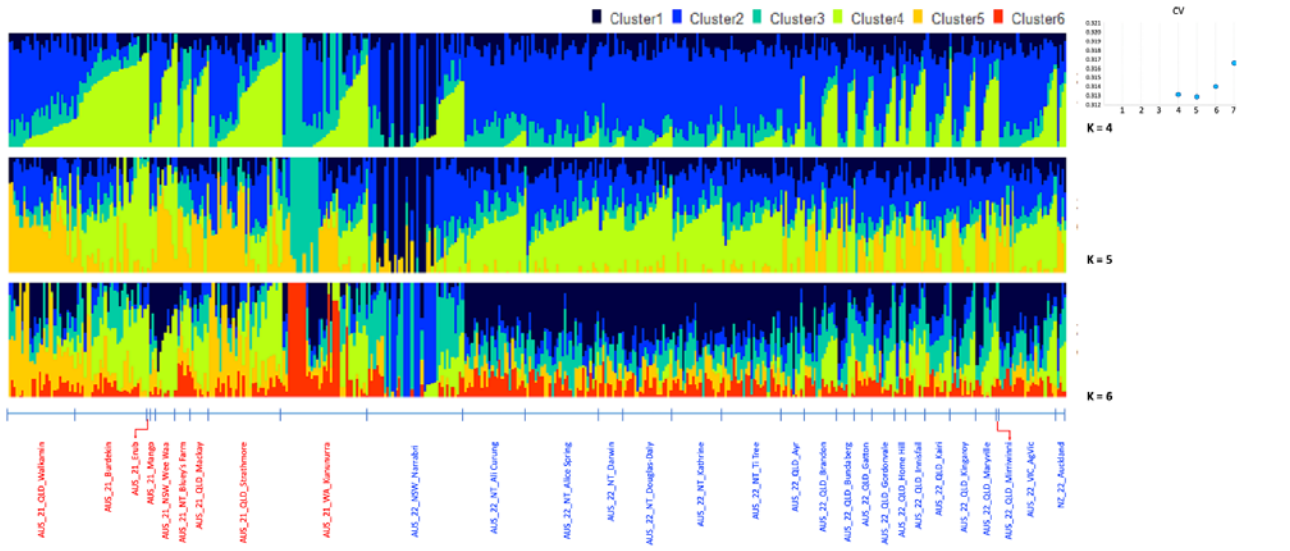


4.2 Admixture analysis

Admixture analysis at K=5 returned the best CV value (Fig. 5) and suggested that the broad clusters in QLD remained largely consistent across populations representing the initial incursion (Fig. 5; labelled in red as AUS_21) and year-2 post incursion (Fig. 5; labelled in blue as AUS_22). However, there appeared to be an enrichment for cluster 4 in QLD, which was predominantly found in the AUS_21_Burdekin population. Cluster 4 has since exhibited strong enrichment in all populations in the AUS_22_NT and contrasting the AUS_21_NT_Bluey's Farm population. For cluster 5, initially present in relatively high abundance across all AUS_21 populations, has reduced in abundance in all AUS_22_NT populations, while persisted in all AUS_22_QLD populations. Finally, the AUS_22_NSW_Narrabri population at K=5 exhibited the most novel genome admixture pattern, especially with cluster 1 but lacking cluster 4 for some samples. There appeared to be two or more separate population clusters in the AUS_22_NSW_Narrabri population, similar to the AUS_21_WA_Kununurra and AUS_21_QLD_Strathmore populations which also appeared to consist of multiple population clusters (see also PCA section, Fig. 6).

We were unable to follow through in the spatial genomic changes in the WA population due to loss of year-2 samples in transit. The unique population clustering at spatial and temporal scales detected in Australia FAW populations sampled during the early stages (i.e., from March 2020 (Rane et al., 2022a) to May 2022 (this study)) highlights the need for ongoing monitoring of population structure and diversity in Australia's agricultural landscape. Admixture analysis based on the 870 nuclear SNP loci is consistent with the mitochondrial haplotype analysis, and suggests that Australia FAW populations involved multiple founders, with a possible explanation being novel and ongoing introduction of genomic compositions (e.g., also evident from the greater C-strain mitogenome diversity detected in AUS_22 samples), even in 2022. The expected population level genome homogenisation at these early stages of the pest's introduction events was not observed between NT and eastern state populations (Fig. 5), highlighting limited inter-population admixture. Additional chromosome level analysis is needed to elucidate kinship, detailed admixture patterns and microspatial gene-flow.

Fig. 5: Admixture analysis of Australia and New Zealand *Spodoptera frugiperda* populations based on 870 single nuclear polymorphism (SNP) loci. Populations representing year-1 incursions have been extensively analysed in Rane et al. (2022a) and are labelled in red as 'AUS_21'. Populations representing post year-1 incursions are labelled in blue as 'AUS_22'. Optimal genetic cluster of K=5 was identified from the CV value. See main text for detailed interpretation.



4.3 Gene flow analysis via F_{ST}

Population gene flow patterns were used to infer population connectivity (i.e., sub-structure) between initial year (i.e., AUS_21) and subsequent (i.e., AUS_22) FAW populations from WA, NT, QLD, NSW, and VIC (Table 3). Overall, and contradictory to the assumption that Australia FAW populations were the result of a single initial Queensland incursion event (e.g., Qi et al., 2021; Wan et al., 2021), gene flow patterns suggested limited population connectivity between various year-1 populations (AUS_21), and between AUS_21 populations vs. most of AUS_22 populations, with most of these pairwise comparisons showing overall high F_{ST} values (i.e., red>orange>yellow colour cells). Furthermore, the NSW and NT AUS_21 populations (from Wee Waa, and Bluey's Farm, respectively; Table 3) remained highly sub-structured when compared with most other Australia FAW populations across both sampling periods (i.e., AUS_21; AUS_22), except Home Hill in QLD and the NZ samples.

AUS_22 NT populations generally showed gene flow with QLD, NSW, and VIC populations, while population substructure in QLD populations was detected, especially for the Home Hill population in QLD. The New Zealand population (see Table S1) which was sampled in April 2022 from Auckland region showed weak population substructure when compared with Australia populations that were sampled between March and May 2020 from Queensland and WA, but lacked evidence of gene flow when compared with Australia FAW populations sampled between January 2021 and May 2022. Concurrently, the NZ and Home Hill populations showed a near equivalent differentiation to extant AUS populations yet remained differentiated when compared to each other.

While low F_{ST} values with other Asian (e.g., China, India) and various SEA populations (e.g., Laos, Myanmar, Malaysia, Philippines, Vietnam) may suggest connectivity with various invasive populations, the small NZ sample (n = 4) nevertheless limited our ability to interpret the extent of gene flow between Australia, SEA and Asia FAW populations. There is also a lack of data to aid our understanding of gene flow between WA FAW populations both at spatial and temporal scales due to the 2nd year samples being lost by the courier company.

When comparing F_{ST} estimates of AUS_21 and AUS_22 populations to the Asian populations, there is an overall reduced differentiation between the AUS_22 populations and Asian populations, compared to the AUS_21 samples. In some cases, AUS_22 populations displayed high similarity to Asian populations than AUS_21 samples from the same state. Finally, it was noted that while the AUS_22 populations had a greater similarity to populations in SEA, the NZ population bears marked genetic similarity to the South Korean population, further highlighting the substructure noted in the recent survey.

4.4 Principal Components analysis

The Principal Components Analysis (PCA) carried out using AUS_21, AUS_22 and NZ samples provided further clarity to support signatures of multiple introductions (Fig. 6). These populations largely clustered together, which is a noticeable behaviour of invasive populations as previously described (Rane et al., 2022a; Tay et al., 2022d).

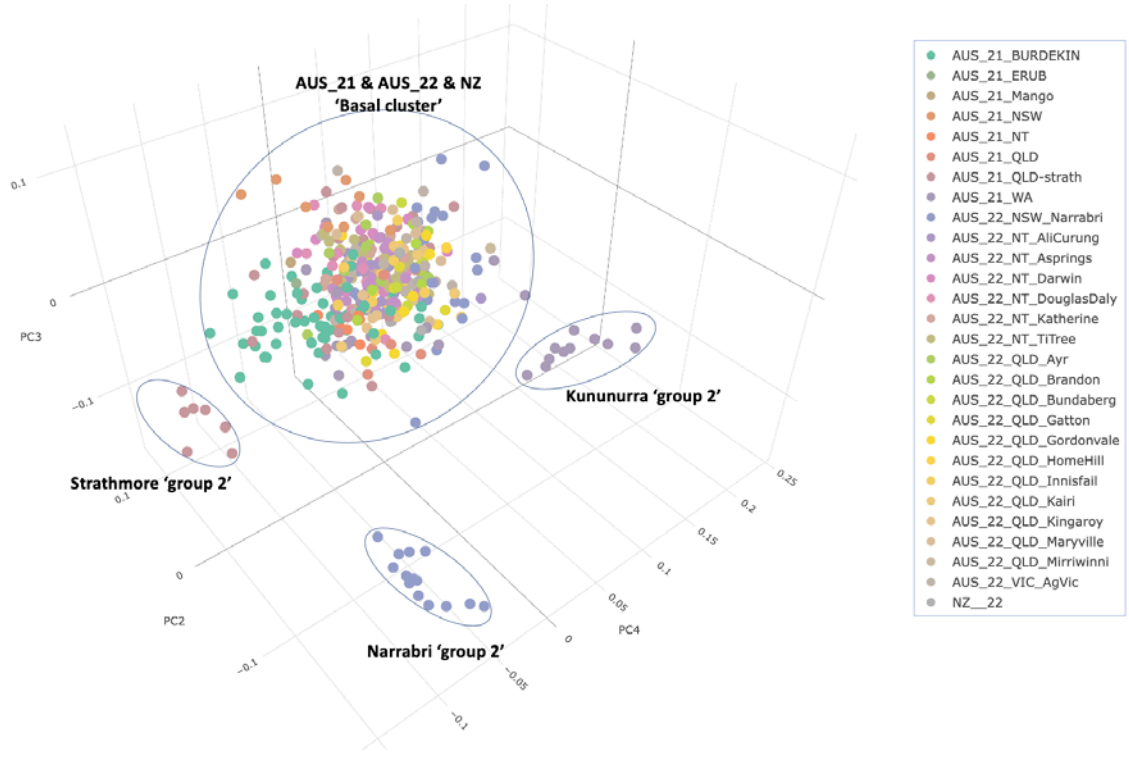
Most significantly, the AUS_21 populations demonstrated a greater spread along the PC's 2 and 3, whereas the AUS_22 populations were largely clustered in the basal cluster. Of note, were the two AUS_21 populations (Strathmore in QLD and Kununurra in WA) that presented satellite clusters (i.e., 'group 2' clusters in Fig. 6), with several samples also present in the basal cluster. In the AUS_22 populations, this behaviour was only demonstrated by the NSW Narrabri population (i.e., Narrabri 'group 2' cluster in Fig. 6), reinforcing the observations from the admixture analysis and F_{ST}'s. The NZ populations were also clustered in the basal cluster, though a sample size of 4 was not sufficient to draw extensive conclusions.

Table 3: F_{ST} estimates of gene flow between Australia FAW populations from 1st year of the pest incursion (AUS_21 samples) and the 2nd year post incursion (AUS_22 samples). F_{ST} estimates are represented by colour heat map (Red>Orange>Yellow>Light Green>Dark Green). Population locations are shown in Fig. 1 and detailed in Rane et al. (2022a) and Tay et al. (2022d).

	AUS_21_NSW-WeeWaa	AUS_21_NT-Bluey's	AUS_21_QLD-Walkamin	AUS_21_QLD-strath	AUS_21_WA_Kununarra	AUS_22_NSW_Narrabri	AUS_22_NT_AliCurung	AUS_22_NT_Asprings	AUS_22_NT_Darwin	AUS_22_NT_DouglasDaly	AUS_22_NT_Katherine	AUS_22_NT_TiTree	AUS_22_QLD_Ayr	AUS_22_QLD_Brandon	AUS_22_QLD_Bundaberg	AUS_22_QLD_Gatton	AUS_22_QLD_Gordonvale	AUS_22_QLD_HomeHill	AUS_22_QLD_Innisfail	AUS_22_QLD_Kairi	AUS_22_QLD_Kingaroy	AUS_22_QLD_Maryville	AUS_22_VIC_AgVic	NZ
AUS_21_BURDEKIN	0.032	0.039	0.006	0.005	0.005	0.016	0.009	0.01	0.005	0.008	0.007	0.007	6E-04	0.004	4E-04	0.004	0.003	0.007	2E-04	0.002	3E-04	0.004	0.006	0.017
AUS_21_NSW-WeeWaa	N/A	0.066	0.022	0.036	0.034	0.05	0.037	0.039	0.032	0.034	0.036	0.036	0.025	0.03	0.023	0.025	0.027	0.015	0.02	0.032	0.03	0.028	0.033	0.01
AUS_21_NT-Bluey's	N/A	N/A	0.037	0.038	0.039	0.054	0.048	0.051	0.039	0.042	0.046	0.045	0.038	0.04	0.029	0.035	0.044	0.024	0.039	0.044	0.04	0.043	0.047	0.024
AUS_21_QLD-Walkamin	N/A	N/A	N/A	6E-04	0.005	0.005	0.004	0.006	0.001	0.002	0.001	4E-04	0.01	0.007	0.01	0.012	0.008	0.02	0.011	0.007	0.01	0.007	0.004	0.029
AUS_21_QLD-strath	N/A	N/A	N/A	N/A	0.012	0.021	0.014	0.016	0.011	0.014	0.013	0.014	0.006	0.008	0.003	4E-04	0.009	8E-04	0.006	0.008	0.004	0.012	0.012	0.013
AUS_21_WA_Kununarra	N/A	N/A	N/A	N/A	N/A	0.017	0.008	0.011	0.006	0.011	0.009	0.008	0.003	0.004	6E-05	0.005	0.004	0.008	0.003	0.004	0.001	0.008	0.008	0.018
AUS_22_NSW_Narrabri	N/A	N/A	N/A	N/A	N/A	N/A	0.006	0.007	0.003	0.007	0.004	0.005	0.002	0.003	0.005	0.006	0.002	0.015	0.002	9E-04	5E-04	0.002	0.004	0.021
AUS_22_NT_AliCurung	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.006	0.011	0.007	0.009	0.008	0.009	0.007	0.014	0.016	0.011	0.018	0.007	0.009	0.012	0.005	0.005	0.026
AUS_22_NT_Asprings	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.01	0.005	0.007	0.006	0.009	0.007	0.011	0.013	0.009	0.018	0.005	0.008	0.01	0.005	0.005	0.025
AUS_22_NT_Darwin	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.013	0.013	0.013	0.017	0.011	0.016	0.017	0.013	0.023	0.01	0.012	0.013	0.013	0.012	0.029
AUS_22_NT_DouglasDaly	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.008	0.015	0.007	0.012	0.011	0.009	0.019	0.01	0.008	0.011	0.006	0.008	0.026
AUS_22_NT_Katherine	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.012	0.007	0.014	0.014	0.012	0.018	0.008	0.009	0.011	0.006	0.007	0.028
AUS_22_NT_TiTree	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.013	0.008	0.013	0.016	0.012	0.021	0.009	0.01	0.011	0.008	0.008	0.029
AUS_22_QLD_Ayr	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.015	0.018	0.021	0.019	0.028	0.02	0.015	0.015	0.016	0.013	0.035
AUS_22_QLD_Brandon	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.018	0.015	0.026	0.017	0.016	0.016	0.011	0.008	0.034
AUS_22_QLD_Bundaberg	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.023	0.021	0.032	0.024	0.022	0.021	0.02	0.013	0.04
AUS_22_QLD_Gatton	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.022	0.033	0.019	0.022	0.024	0.017	0.014	0.041
AUS_22_QLD_Gordonvale	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.029	0.022	0.016	0.019	0.017	0.012	0.039
AUS_22_QLD_HomeHill	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.025	0.025	0.024	0.029	0.021	0.047
AUS_22_QLD_Innisfail	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.018	0.019	0.01	0.04
AUS_22_QLD_Kairi	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.019	0.013	0.01	0.039
AUS_22_QLD_Kingaroy	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.011	0.035
AUS_22_QLD_Maryville	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.008	0.034
AUS_22_VIC_AgVic	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.03

Note: No Statistical tests were enforced here due to overall smaller population sizes in many sub-populations. The Hudson correction should account for it since it incorporates a Fishers exact test. For F_{ST} estimates involving New Zealand (NZ) samples please see the full F_{ST} table in Table S1.

Fig. 6: Principal Component Analysis (PCA) of *Spodoptera frugiperda* (FAW) populations from Australia (AUS_21, AUS_22) and New Zealand.



5 CONCLUSION

This study identified unique C- and R-strain mitogenomes in recent AUS_22 populations to highlight the diverse FAW population compositions across its Old World invasive ranges. The findings also supported potential on-going movements of FAW between Asia/SEA and Australia. Admixture analyses showed that there were unique genetic clusters in both AUS_21 and AUS_22 populations, while the expected homogenisation of AUS_21 and AUS_22 populations based on the widely assumed rapid spread of the pest was not realised, at least for Australia scenarios. Australia and New Zealand populations continued largely as C- and R-strain hybrids, although some individuals from WA (AUS_21) and from NSW (AUS_22) appeared to lack hybrid signatures. Furthermore, admixture analyses also identified unexplained genetic clusters in, e.g., Kununurra WA, Strathmore QLD, and Narrabri NSW (Fig. 5; see also Fig. 6 of PCA)). QLD AUS_22 populations showed the highest similarity to extant AUS_21 populations as seen from the cluster composition and following analyses. Therefore, of all the populations in Australia, AUS_22 populations from QLD are the only populations with a strong signature of being derived from AUS_21 populations, with few exceptions. These patterns also suggest that the population composition is highly dynamic and fluid, given the lack of consistency between genomic surveys in consecutive years.

F_{ST} analysis suggested movements of NT populations into QLD populations while there was a general lack of admixing within the QLD populations. Microspatial gene flow analysis using high chromosomal delineated density genomic markers would be needed to further dissect this observation. Patterns of pairwise F_{ST} also indicated the presence of four outliers (AUS_21: Bluey's Farm and Wee Waa; AUS_22: Home Hill and NZ). These populations bore little to no similarities to existing AUS populations, but showed a similar pattern of differentiation across the study samples. This could indicate bridge-head populations in Asia/SEA that are focal points of FAW population movement towards Australia/NZ (Guillemaud et al., 2011; Rane et al., 2022a). Diverse insecticide resistance alleles and resistance profiles have been reported in Africa and Asia FAW populations (e.g., Boaventura et al., 2020; Deshmukh et al., 2020; Eriksson, 2019; Guan et al., 2021; Lv et al., 2021; Zhang et al., 2020), and more recently also reported in WA and QLD populations based on bioassay studies and whole genome analyses (Tay et al., 2022c). This population genomic study of post year-1 incursion of FAW in Australia therefore further provided evidence to demonstrate the significant genetic diversity in invasive FAW populations across Africa and Asia/Pacific regions. This high genetic diversity profile of invasive-range FAW is congruent to the signature of multiple introductions (e.g., Arnemann et al., 2019; Jiang et al., 2022; Jones et al., 2019; Tay & Gordon, 2019; Tay et al., 2022c; Tay et al., 2022d), and further supported the need to improve regional biosecurity capacity, given the likely on-going introduction into Australia of populations with novel genomic compositions that could include genes of economic and biosecurity importance, including better adaptation to diverse ecoclimatic conditions in new geographic habitats.

Existing SEA/Australia FAW genomic results suggest multiple introgression events into Australia and evolving substructure in the region (Rane et al., 2022a). Increasingly for globally significant agricultural pest species (e.g., Anderson et al., 2016; Arnemann et al., 2019; Elfekih et al., 2018; Gilligan et al., 2019; Jones et al., 2019; Lopes-da-Silva et al., 2014; Pozebon et al., 2020; Tay & Gordon, 2019; Tay et al., 2017) and including also the fall armyworm, analysis of whole genome data is supporting persistent human-assisted introductions even after initial detections, such as in China (Jiang et al., 2022), Africa (Nagoshi et al., 2019a; Rane et al., 2022a; Schlum et al., 2021; Tay et al., 2022d), and in SEA (e.g., in Malaysia; Rane et al., 2022a). This study of multiple timeline populations in Australia represents one of the few studies to further demonstrate the importance of on-going monitoring of pest populations at the genomic level. For Australia and New Zealand, this will necessarily also include follow-up studies of FAW populations in the SEA and the Indo-Pacific regions. While we have provided preliminary genomic composition of limited numbers of New Zealand individuals to infer the pest's invasion biology, more samples are needed to better elucidate its introduction pathways into the country, as well as to better understand the evolutionary and adaptation potentials of the pest in New Zealand.

To better understand the FAW's ability to rapidly adapt to localised pest management strategies will require selective sweep analyses as well as episodic selection analysis. Such an analysis would require access to

comparable global whole genome datasets to differentiate between episodic selection and alleles that appear under selection, but were instead the result of migration (Messer & Petrov, 2013). Selective sweep analyses of populations from Australia and surrounding regions (e.g., China, India, Indonesia, Thailand) will be needed to further assist with developing relevant management solutions to bolster the resilience of Australia's and regional agricultural industries. While the genome dataset generated in some recent studies have been made available (e.g., Guan et al., 2021; Gui et al., 2020; Rane et al., 2022a; Schlum et al., 2021; Tay et al., 2022c; Tay et al., 2022d), other whole genome datasets remained unavailable despite publication status and repeated requests (e.g., Yainna et al., 2021; Zhang et al., 2020). Future research should therefore target populations where data is currently lacking, to enable understanding of the genomic of adaptation by the FAW and elucidating microspatial pathways of movement/incursions.

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Table S1: Full F_{ST} values of FAW populations from Australia (AUS_21, AUS_22), New Zealand, and SEA as reported in (Rane et al., 2022a).

CORRECTED	AUS_21_NSW-WeeWaa	AUS_21_NT-Bluey's	AUS_21_QLD-Walkamin	AUS_21_QLD-strath	AUS_21_WA_Kununarra	AUS_22_NSW_Narrabri	AUS_22_NT_AliCurung	AUS_22_NT_Asprings	AUS_22_NT_Darwin	AUS_22_NT_DouglasDaly	AUS_22_NT_Katherine	AUS_22_NT_TiTree	AUS_22_QLD_Ayr	AUS_22_QLD_Brandon	AUS_22_QLD_Bundaberg	AUS_22_QLD_Gatton	AUS_22_QLD_Gordonvale	AUS_22_QLD_HomeHill	AUS_22_QLD_Innisfail	AUS_22_QLD_Kairi	AUS_22_QLD_Kingaroy	AUS_22_QLD_Maryville	AUS_22_VIC_AgVic	CN_CY	CN_XP	CN_YJ	IND	LAO	MAL	MYM	MYS	NZ	PHL	PNG	SKOR	VIET
AUS_21_BURDEKIN	0.032	0.039	0.006	0.005	0.005	0.016	0.009	0.010	0.005	0.008	0.007	0.007	0.001	0.004	0.000	0.004	0.003	0.007	0.000	0.002	0.000	0.004	0.006	0.010	0.013	0.002	0.002	0.005	0.009	0.005	0.015	0.017	0.011	0.005	0.014	0.002
AUS_21_NSW-WeeWaa	N/A	0.066	0.022	0.036	0.034	0.050	0.037	0.039	0.032	0.034	0.036	0.036	0.025	0.030	0.023	0.025	0.027	0.015	0.020	0.032	0.030	0.028	0.033	0.045	0.044	0.038	0.033	0.023	0.029	0.024	0.037	0.010	0.028	0.026	0.040	0.018
AUS_21_NT-Bluey's	N/A	N/A	0.037	0.038	0.039	0.054	0.048	0.051	0.039	0.042	0.046	0.045	0.038	0.040	0.029	0.035	0.044	0.024	0.039	0.044	0.040	0.043	0.047	0.056	0.053	0.046	0.044	0.040	0.042	0.037	0.053	0.024	0.041	0.030	0.052	0.035
AUS_21_QLD-Walkamin	N/A	N/A	N/A	0.001	0.005	0.005	0.004	0.006	0.001	0.002	0.001	0.000	0.010	0.007	0.010	0.012	0.008	0.020	0.011	0.007	0.010	0.007	0.004	0.006	0.006	0.001	0.008	0.003	0.003	0.009	0.006	0.029	0.001	0.005	0.008	0.007
AUS_21_QLD-strath	N/A	N/A	N/A	N/A	0.012	0.021	0.014	0.016	0.011	0.014	0.013	0.014	0.006	0.008	0.003	0.000	0.009	0.001	0.006	0.008	0.004	0.012	0.012	0.013	0.018	0.008	0.008	0.011	0.011	0.009	0.023	0.013	0.015	0.010	0.014	0.008
AUS_21_WA_Kununarra	N/A	N/A	N/A	N/A	N/A	0.017	0.008	0.011	0.006	0.011	0.009	0.008	0.003	0.004	0.000	0.005	0.004	0.008	0.003	0.004	0.001	0.008	0.008	0.014	0.014	0.006	0.003	0.007	0.015	0.006	0.016	0.018	0.012	0.007	0.020	0.004
AUS_22_NSW_Narrabri	N/A	N/A	N/A	N/A	N/A	N/A	0.006	0.007	0.003	0.007	0.004	0.005	0.002	0.003	0.005	0.006	0.002	0.015	0.002	0.001	0.000	0.002	0.004	0.016	0.020	0.010	0.007	0.013	0.020	0.014	0.024	0.021	0.023	0.015	0.031	0.012
AUS_22_NT_AliCurung	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.006	0.011	0.007	0.009	0.008	0.009	0.007	0.014	0.016	0.011	0.018	0.007	0.009	0.012	0.005	0.005	0.010	0.015	0.001	0.001	0.005	0.009	0.007	0.017	0.026	0.012	0.006	0.025	0.004
AUS_22_NT_Asprings	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.010	0.005	0.007	0.006	0.009	0.007	0.011	0.013	0.009	0.018	0.005	0.008	0.010	0.005	0.005	0.011	0.015	0.001	0.001	0.007	0.011	0.009	0.017	0.025	0.016	0.009	0.026	0.005
AUS_22_NT_Darwin	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.013	0.013	0.013	0.017	0.011	0.016	0.017	0.013	0.023	0.010	0.012	0.013	0.013	0.012	0.008	0.014	0.003	0.004	0.003	0.001	0.001	0.006	0.029	0.007	0.000	0.020	0.006
AUS_22_NT_DouglasDaly	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.008	0.015	0.007	0.012	0.011	0.009	0.019	0.010	0.008	0.011	0.006	0.008	0.012	0.018	0.002	0.003	0.000	0.002	0.002	0.010	0.026	0.010	0.001	0.024	0.003
AUS_22_NT_Katherine	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.012	0.007	0.014	0.014	0.012	0.018	0.008	0.009	0.011	0.006	0.007	0.010	0.015	0.003	0.001	0.002	0.007	0.005	0.013	0.028	0.011	0.005	0.021	0.001
AUS_22_NT_TiTree	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.013	0.008	0.013	0.016	0.012	0.021	0.009	0.010	0.011	0.008	0.008	0.011	0.015	0.002	0.000	0.002	0.007	0.004	0.013	0.029	0.012	0.004	0.024	0.001
AUS_22_QLD_Ayr	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.015	0.018	0.021	0.019	0.028	0.020	0.015	0.015	0.016	0.013	0.006	0.007	0.006	0.002	0.005	0.000	0.000	0.006	0.035	0.005	0.003	0.014	0.007
AUS_22_QLD_Brandon	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.018	0.015	0.026	0.017	0.016	0.016	0.011	0.008	0.003	0.006	0.003	0.005	0.002	0.008	0.002	0.013	0.034	0.012	0.003	0.018	0.001
AUS_22_QLD_Bundaberg	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.023	0.021	0.032	0.024	0.022	0.021	0.020	0.013	0.001	0.003	0.006	0.010	0.004	0.003	0.001	0.006	0.040	0.007	0.003	0.013	0.005
AUS_22_QLD_Gatton	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.022	0.033	0.019	0.022	0.024	0.017	0.014	0.001	0.003	0.011	0.014	0.001	0.003	0.001	0.010	0.041	0.005	0.003	0.010	0.002
AUS_22_QLD_Gordonvale	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.029	0.022	0.016	0.019	0.017	0.012	0.003	0.006	0.005	0.007	0.003	0.004	0.002	0.009	0.039	0.007	0.002	0.018	0.005
AUS_22_QLD_HomeHill	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.025	0.025	0.024	0.029	0.021	0.006	0.004	0.012	0.021	0.010	0.001	0.012	0.005	0.047	0.001	0.006	0.008	0.012
AUS_22_QLD_Innisfail	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.018	0.019	0.010	0.000	0.002	0.004	0.010	0.003	0.004	0.002	0.009	0.040	0.006	0.001	0.015	0.004
AUS_22_QLD_Kairi	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.019	0.013	0.010	0.001	0.005	0.005	0.007	0.003	0.010	0.002	0.013	0.039	0.011	0.005	0.017	0.000
AUS_22_QLD_Kingaroy	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.018	0.011	0.002	0.005	0.007	0.009	0.002	0.006	0.000	0.010	0.035	0.007	0.000	0.017	0.005
AUS_22_QLD_Maryville	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.008	0.006	0.009	0.003	0.006	0.001	0.005	0.003	0.011	0.034	0.008	0.003	0.019	0.002
AUS_22_VIC_AgVic	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.012	0.001	0.003	0.001	0.005	0.003	0.013	0.030	0.010	0.004	0.021	0.002
CN_CY	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.004	0.005	0.005	0.016	0.012	0.016	0.026	0.019	0.021	0.018	0.024	0.014
CN_XP	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.003	0.003	0.019	0.014	0.015	0.027	0.018	0.022	0.019	0.025	0.013
CN_YJ	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.010	0.008	0.002	0.010	0.017	0.024	0.014	0.008	0.017	0.005
IND	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.004	0.001	0.003	0.015	0.030	0.012	0.008	0.018	0.001
LAO	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.001	0.007	0.003	0.016	0.002	0.003	0.019	0.012
MAL	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.001	0.012	0.013	0.008	0.004	0.021	0.004
MYM	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.005	0.017	0.002	0.004	0.016	0.011
MYS	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.011	0.013	0.009	0.028	0.000
NZ	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.009	0.015	0.001	0.020
PHL	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.004	0.020	0.001
PNG	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.017	0.009
SKOR	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.010

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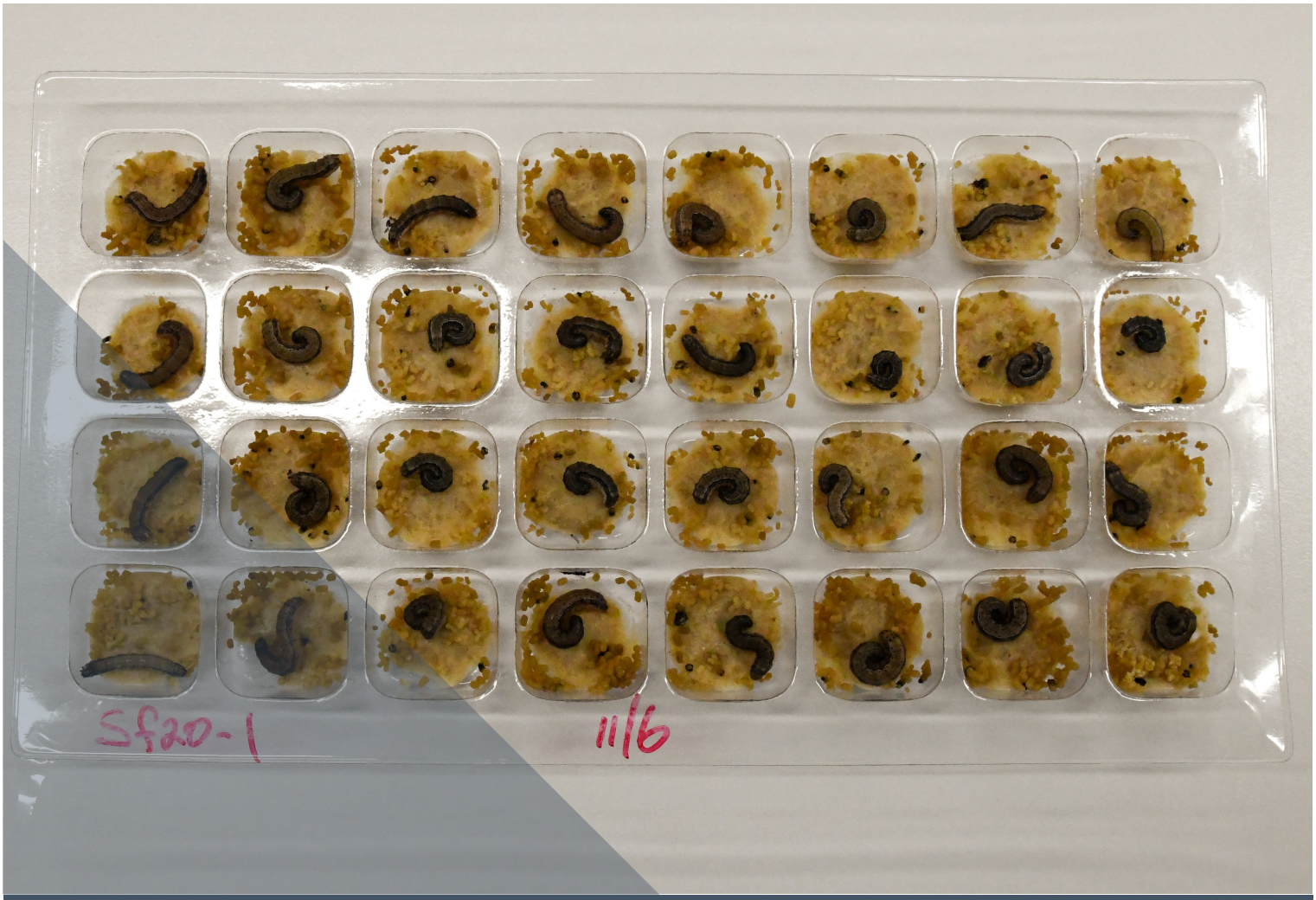

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