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Microbiome composition of Drosophila suzukii varies across geographical regions

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Drosophila suzukii is a common agricultural pest in numerous parts of the world, costing more than \$500 million annually in crop loss in the United States alone. Understanding the genetic and physiological mechanisms underlying its remarkable adaptability has been a major focus for the agricultural industry as well as evolutionary biologists. The microbiome, the community of microbes associated with host organisms, can play a pivotal role in local adaptation by improving host resilience to environmental stress and providing access to new sources of nutrition. Here, we test the hypothesis that the colonization of nonnative regions is associated with the incorporation of regionally-specific microbial taxa. We compare the microbiome profiles of wild-caught D. suzukii across five global sites, Asia, Europe, the United Kingdom, North America, and Hawai'i. We also compare microbial communities of D. suzukii found in Hawai'i to another local invasive species, D. immigrans, and native Hawaiian drosophilids. Our results reveal that wild-caught D. suzukii from Asia, Europe, the United Kingdom, North America, and the Hawaiian Islands exhibit distinct microbial compositions indicating that the environment is a stronger driver of microbiome composition than species identity. Seven bacterial families were conserved between all wild D. suzukii populations. Within Hawai'i, non-native D. suzukii bacterial communities differed from those of native Hawaiian Drosophila species as well as non-native D. immigrans. By contrast, fungal microbiome profiles between the Hawaiian Drosophila and two invasive species closely resemble each other. In sum, all populations of D. suzukii in this study contain a subset of conserved bacterial families but also incorporate local bacterial taxa. This strategy may contribute to the rapid range expansion of D. suzukii and enhance its ability to exploit new dietary sources.

KEYWORDS

Drosophila immigrans, Hawaiian Drosophila, mycobiome, fungal microbiome, microbial diversity

Introduction

The spotted wing Drosophila, Drosophila suzukii, is considered a globally invasive pest, having spread from its native range in East Asia (Kanzawa, 1939; Bolda et al., 2010) to disparate locations in North America (Hauser, 2011), Europe (Calabria et al., 2012), South American (Deprá et al., 2014; Andreazza et al., 2017), North African countries (Kwadha et al., 2021), and Asia (Calabria et al., 2012; Cini et al., 2012). D. suzukii's preference to oviposit in soft-flesh fruits has resulted in significant yield losses of fruit crops including cherries, grapes, and plums (Tait et al., 2021). The success of D. suzukii in expanding its range is partly attributed to its high adaptability to novel habitats and ecological niches (Poyet et al., 2015; Little et al., 2020). Within Hawai'i, the species is found across the islands of Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i Island (Kaneshiro, 1983; Leblanc et al., 2009; Hauser, 2011) in lower elevation agricultural parks as well as high elevation native forest reserves. D. suzukii is capable of thriving in elevations over 2000 m, and at mean annual temperatures of less than 12 °C (Sánchez-Ramos et al., 2019a, b; Curbelo et al., 2022), near the lowest temperatures considered viable for activity in this genus (Koštál et al., 2016). In addition, D. suzukii has been observed feeding on a variety of native and non-native fruits (Magnacca et al., 2008; Koch et al., 2020). Previous genetic analyses of D. suzukii populations from Asia (Feng et al., 2024), Hawai'i (Koch et al., 2020), the continental United States (Mérel et al., 2021), Europe, and South America (Adrion et al., 2014) identified genetic divergences that may facilitate successful environmental adaptation. The microbiome has also been hypothesized as a major driver of local evolution allowing organisms to exploit new ecological niches by enhancing host physiology and behavior (Shu et al., 2021). Indeed, the ability to consume novel foods in a newly colonized area has been proposed as a key factor for successful invasion (Shik and Dussutour, 2020). D. suzukii uses microbes to aid metabolism and survival in their preferred high-sugar and low-protein fruit hosts (Bing et al., 2018; Gao et al., 2023) and may use naturally occurring microbes on a new host plant to extract essential nutrients (Lin et al., 2021). Local microbes may also aid in the tolerance of temperatures near the extreme of their ranges (Mueller et al., 2011; Chevalier et al., 2015; Houwenhuyse et al., 2021).

To address the possibility that the colonization of new ecological niches by *D. suzukii* is associated with changes in microbiome composition, we compared bacterial profiles of wild *D. suzukii* populations from the native ranges in China and Japan to populations from non-native ranges in Europe, the United Kingdom (UK), North America, and Hawai'i (Martinez-Sañudo et al., 2018) and lab-reared *D. suzukii* from the United States (US) (Bing et al., 2018; Martinez-Sañudo et al., 2018; Lin et al., 2021). To assess how closely *D. suzukii* microbiomes resembles that of other native and invasive species found in similar habitats, we compared Hawaiian *D. suzukii* bacterial and fungal profiles to another cosmopolitan drosophilid found in Hawai'i, *D. immigrans*, as well as to native Hawaiian picture-wing *Drosophila*.

Materials and methods

Sample collection of drosophilids in the Hawaiian Islands

D. suzukii, *D. immigrans*, and endemic Hawaiian drosophilidae were collected from the islands of Moloka'i, Lana'i, and Hawai'i Island using sponges baited with mushrooms, banana, and yeast. Samples were immediately placed into 95% ethanol, transported on ice packs, and stored at -80 °C in the laboratory until processing. Metadata associated with samples collected in Hawai'i are provided in Supplementary Tables S1, S2.

Library preparation and sequencing of Hawaiian dosophilidae

Details of DNA extraction and library preparation are as previously described (Medeiros et al., 2025). Briefly, surfacesterilized flies were homogenized using a bead mill homogenizer (Bead Ruptor Elite, Omnic, Inc; GA, USA) and DNA extracted with PowerMag Bead Solution kit (Qiagen; MD, USA) according to manufacturer's instructions. The 16S rRNA gene was amplified with primers to the V4 region (515F: GTGYCAGCMGCCGCGGTAA; 806R: GGACTACNVGGGTWTCTAAT) (Parada et al., 2016). Fungal diversity was characterized using primers to the internal transcribed spacer (ITS1f: CTTGGTCATTTAGAGGAAGTAA; ITS2: GCTGCGTTCTTCATCGATGC) (White et al., 1990). The primers contain a 12-base pair Golay-indexed code for demultiplexing. The PCRs were performed with the KAPA3G Plant kit (Sigma Aldrich, MO, USA) using the following parameters: 95 °C for 3 min, followed by 35 cycles of 95 °C for 20 seconds, 50 °C for 15 seconds, 72 °C for 30 seconds, and a final extension for 72 °C for 3 min. The PCR products were cleaned and normalized with the Justa-plate kit (Charm Biotech, MO, USA). High throughput sequencing (HTS) was performed with MiSeq and 250 bp paired-end kits (Illumina, Inc., CA, USA).

Data processing of 16S rRNA amplicons for multi-region comparisons

Taxonomic analyses of *D. suzukii, D. immigrans*, and native Hawaiian *Drosophila* microbiomes were assessed from next-generation amplicon sequencing of regions in the 16S rRNA gene using DADA2 v1.16 (Callahan et al., 2016). All analyses were conducted using *R version 4.4.2* (R Core Team, 2022). Four publicly accessible projects deposited on the NCBI Sequence Read Archive (SRA, https://www.ncbi.nlm.nih.gov/sra) and in-house data derived from *D. suzukii, D. immigrans*, and native Hawaiian *Drosophila* collected in Hawai'i by the authors of this study were used in the analysis for a total of five independent sources of sequencing data (Supplementary Table S3). FASTQ files deposited

onto the SRA were retrieved using fasterqdump command, part of the NCBI SRA Toolkit. SRA projects included in this study are PRJEB50289 (Fountain et al., 2018), PRJNA347319 (Martinez-Sañudo et al., 2018), PRJNA412893, and PRJNA719706 (Lin et al., 2021). All raw sequence reads were demultiplexed before analysis.

All sequence data were generated from paired-end Illumina sequencing strategy, however there was no consensus in the primer sets used for all projects. Additionally, two of the SRA projects (PRJNA347319 and PRJNA719706) reported paired-end read strategy but only one spot contained read information from the SRA database; thus, only one file per sample was extracted. Visualization of the quality profile plots of these data revealed that the SRA data contained merged forward and reverse reads, referred to herein as extended fragments. Due to the unique nature of each dataset used in this study, each project was handled separately for pre-processing. A custom R script was used to search for the presence of sequencing primers in the reads. Sequencing primers were reported for all but SRA projects PRJNA412893, and in this case the primers used were inferred using the custom script to search for common 16S rRNA sequencing primers until the primer sites were identified. Locations of the primer sites in the forward and reverse reads were used to define the trimming (trimLeft) and the quality plots were used to define the truncation (truncLen) filtering parameters in DADA2. A default max EE setting of 2 was used for both forward and reverse reads, but one project required raising the threshold to recover enough sequence reads passing the filter. For extended fragments, as suggested by the DADA2 creator on github, the error rates were inflated by 3 to account for the heterogeneity between the merged subsegments using the command inflateErr. Project-specific details including primers, and pre-processing parameters are given in Supplementary Table S4.

After filtering, trimming and estimating error rates, paired-end reads were merged following the standard DADA2 workflow. Only merged reads or extended fragments (i.e., previously merged reads) were used for downstream analysis. The merged reads (and extended fragments) for 16S rRNA gene sequences from all five projects were used to create a sequence table, remove chimeras and assign taxonomy (excluding mitochondria and chloroplasts) using the SILVA SSU Ref NR database version 138.1 (Quast et al., 2013; Yilmaz et al., 2014). The number of reads tracked through the processing pipeline for each *D. suzukii* sample is given in Supplementary Table S5. Taxonomy assignments for 16S rRNA reads were based on amplicon sequence variant (ASV) data (100% similarity). Each sample was rarefied with a subsampling depth of 5,000 ASVs.

Data processing of ITS amplicons from Hawai'i drosophilidae samples

Post-processing of HTS data (filtering, trimming, and clustering) for Hawai'i samples (native Hawaiian flies, *D. immigrans*, *D. suzukii*) was performed using the "MetaFlow|mics"

Fungal ITS pipeline for fungi which uses the DADA2 workflow (Arisdakessian et al., 2020; Medeiros et al., 2024). ASV clustering was performed at the 97% similarity threshold. Taxonomy assignments for ITS reads were performed with NCBI BLAST, UNITE (Nilsson et al., 2019), and MycoBank (Robert et al., 2013) using a >95% sequence similarity cutoff.

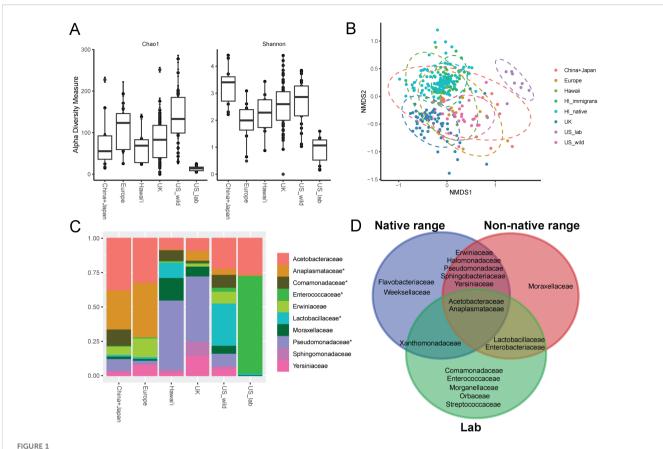
Statistical analysis

To quantify alpha-diversity, we used Chao1 and Shannon index. To assess beta-diversity, we used Bray-Curtis dissimilarity and performed ordination analyses with non-metric multidimensional scaling (NMDS). Analysis of Similarity (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA) tests were applied to test for significant differences in community composition. Analyses were performed after clustering at the family or genus level and using *R* version 4.4.1, and the *phyloseq* package (McMurdie and Holmes, 2013). Venn diagrams were generated using complete sample sets for each population and based on the top ten families for *each* population (https://bioinformatics.psb.ugent.be/webtools/Venn/).

Results

Comparison of bacterial microbiomes of *D. suzukii* across native and invasive ranges and lab-maintained populations

To perform a multi-region comparison of D. suzukii microbiomes, we analyzed the bacterial communities of samples collected from China, Japan, North America, Europe, the UK and Hawai'i. In terms of alpha-diversity, populations from the native range tended to have higher compositional richness and evenness compared to Europe, UK, and Hawai'i when grouped by family (Figure 1A, Table 1). In addition, almost all populations of D. suzukii exhibit distinct compositional profiles (ANOSIM p = 0.001, R = 0.61; Figure 1B, Table 2). However, one exception to this general pattern is that D. suzukii from the native ranges of China and Japan and the non-native range of Europe exhibited similar compositions (PERMANOVA p = 0.075; Table 2). Flies collected in Hawai'i, regardless of species, clustered together in the NMDS ordination plot (Figure 1B) although D. suzukii from Hawai'i differed significantly in compositional profile from other Hawaiian populations (PERMANOVA, p = 0.001; Table 2). Only two bacterial families were unique to flies collected in their native range of China and Japan (Flavobacteriaceae and Weeksellaceae), suggesting that this cosmopolitan species associates with microbes beyond those that are specific to its region of origin. Seven bacterial families were common to all wild-caught D. suzukii, potentially serving as a core microbial community: Acetobacteraceae, Anaplasmatacea, Erwiniaceae, Halomonadaceae, Pseudomonadacae, Sphingobacteriaceae, and Yersiniaceae (Figures 1C, D). At the genus level, only the



Bacterial community profiles of *D. suzukii* populations from native and non-native ranges, and lab settings. Outcomes of statistical comparisons are detailed in Tables 1, 2. (A) Alpha-diversity analyses based on ASVs from wild and lab populations from all sites. Each point represents a single fly. (B) Non-metric multidimensional scaling (NMDS) plot depicting Bray-Curtis dissimilarity distances for wild and lab populations from all sites; ANOSIM p = 0.001, R = 0.61. Each point represents a single fly. Populations are compared at the family level. Ellipses represent 95% confidence intervals. (C) Relative abundance plots of the 10 most abundant bacterial families common to all sites; *: taxa that differed significantly (f-test, p < 0.0001). (D) Venn diagram based on the 10 most abundant taxa for each population showing overlapping bacterial families; native range: n = 8, non-native range: n = 110, lab: n = 16 for all analyses.

endosymbiont *Wolbachia* was common to lab and wild flies (Supplementary Figure S2, Supplementary Table S6).

The bacterial community richness of lab populations was significantly lower compared to each of the wild populations, consistent with previous studies (Chandler et al., 2011; Staubach et al., 2013) (Figure 1A, Table 1). Lab flies from US, China, and Italy contained distinct communities of bacteria, with each profile correlating with geographical location (ANOSIM p=0.001 R = 0.78; Supplementary Figure S1, Supplementary Table S7). However, there were only modest differences in terms of alphadiversity (Supplementary Table S7).

Bacterial and fungal gut microbiome comparison of native Hawaiian *Drosophila, D. immigrans* in Hawaii, and *D. suzukii* in Hawaii

We predicted that *D. suzukii* colonization of new ecological niches may rely on the incorporation of local microbes. To test this possibility, we compared the bacterial and fungal profiles of

D. suzukii to another invasive species established in Hawai'i, D. immigrans, as well as to native Hawaiian Drosophila found at the same sites. In terms of community richness (Chao1), both invasive species exhibited significantly lower bacterial alpha-diversity compared to native flies (Figure 2A, Table 3). However, for fungal profiles, no significant differences in alpha-diversity were found between the three populations (Figure 2D, Table 3). Additionally, D. suzukii contained distinct bacterial communities compared to either D. immigrans or native Hawaiian flies at both family (ANOSIM p = 0.003, R = 0.18; Figure 2G) and genus levels (ANOSIM p = 0.012, R = 0.15; Supplementary Figure S2, Supplementary Table S6). Five families were found in D. suzukii that were not common to other Hawaiian populations. Of these, Rhizobiaceae was also not detected in D. suzukii from other regions and may reflect enrichment from the local environment. At the genus level, Citrobacter and Zymobacter appear to be enriched only in D. suzukii found in Hawai'i and no other Hawaiian populations or regions (Supplementary Figure S2). Four bacterial families were common to invasive and native species in Hawai'i whereas a single family is found in both invasive species, Moraxellaceae (Figure 2G). The presence of the Moraxellaxeae family in both Hawai'i D.

TABLE 1 *P-value* outcomes of pairwise alpha-diversity comparisons at the family level amongst *D. suzukii* multi-regional populations shown in Figure 1A.

Group 1 ¹	Group 2	Alpha-diversity ²		
		Chao1	Shannon	
Europe	China + Japan	0.152	0.002	
Hawai'i	China + Japan	0.941	0.021	
Hawai'i	Europe	0.153	0.456	
UK	China + Japan	0.447	0.021	
UK	Europe	0.152	0.045	
UK	Hawai'i	0.367	0.003	
US_wild	China + Japan	0.014	0.095	
US_wild	Europe	0.423	0.021	
US_wild	Hawai'i	0.003	0.172	
US_wild	UK	0.001	0.250	
US_wild	US_lab	0.001	0.001	
US_lab	China + Japan	0.001	0.001	
US_lab	Europe	0.001	0.005	
US_lab	Hawai'i	0.001	0.001	
US_lab	UK	0.001	0.001	

¹Europe sites consist of Italy, France, Slovenia, Switzerland, and Spain; US_wild sites consist of New York and California; US lab sites consist of New York and California.

immigrans and *D. suzukii* as well as *D. suzukii* populations outside of its native range may indicate a conserved ecological association with invasive drosophilids.

With respect to the fungal microbiome, native Hawaiian flies and both invasive populations exhibited similar profiles in terms of taxonomic composition (ANOSIM p = 0.01, R = 0.117) and alphadiversity (Figure 2). Native and invasive species share five fungal families. As with bacteria, three fungal families appear unique to D. suzukii: Cordycipitaceae, likely a Diptera pathogen (Naranjo-Lázaro et al., 2014), Bulleribasidiaceae, which in its yeast state is used by D. suzukii as a food source (Jiménez-Padilla et al., 2020), and Chrysozymaceae, a yeast previously identified from ghost moth gut (Thitarodes sp.) (Liu et al., 2021).

Discussion

Microbes sourced from the local environment play myriad roles in host physiology including nutrient scavenging (Yamada et al., 2015; Bing et al., 2018), toxin inactivation (Kohl et al., 2014; Zhang et al., 2024), stress resilience (Houwenhuyse et al., 2021; Tefit et al., 2023; Price et al., 2025), lipid metabolism, and sleep regulation (Tefit et al., 2023). Given the broad range and global invasion of *D. suzukii*, we hypothesized that local microbial associations might accompany colonization and regional establishment. Specifically, we predicted that microbiomes of *D. suzukii* from different sites

TABLE 2 *P-value* outcomes of pairwise beta-diversity comparisons at the family level amongst *D. suzukii* multi-regional populations and Hawai'i native and non-native flies shown in Figure 1B.

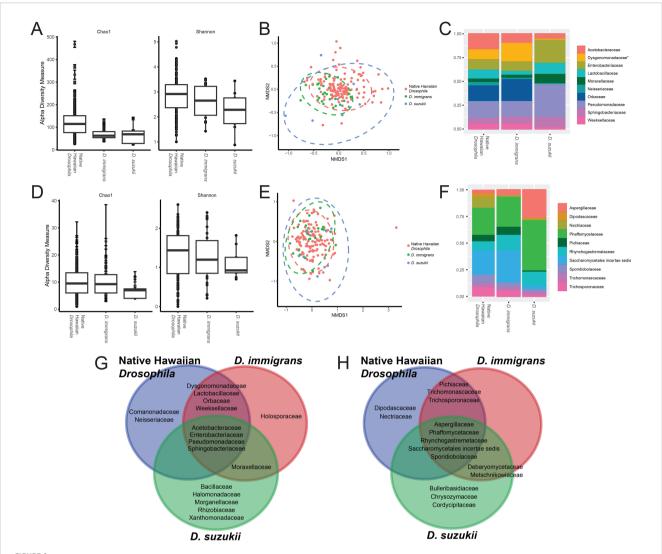
Group 1 ¹	Group 2	Beta-diversity ²
Europe	China + Japan	0.075
Hawai'i	^	0.013
	China + Japan	
Hawaiʻi	Europe	0.002
UK	China + Japan	0.001
UK	Europe	0.001
UK	Hawaiʻi	0.002
US_wild	China + Japan	0.001
US_wild	Europe	0.010
US_wild	Hawaiʻi	0.001
US_wild	UK	0.001
US_wild	US_lab	0.001
US_lab	China + Japan	0.001
US_lab	Europe	0.001
US_lab	Hawaiʻi	0.001
US_lab	UK	0.001
HI_immigrans	China + Japan	0.001
HI_immigrans	Europe	0.001
HI_immigrans	US_wild	0.001
HI_immigrans	UK	0.001
HI_immigrans	HI_native	0.080
HI_immigrans	Hawaiʻi	0.001
HI_immigrans	US_lab	0.001
HI_native	China + Japan	0.001
HI_native	Europe	0.001
HI_native	US_wild	0.001
HI_native	UK	0.001
HI_native	Hawaiʻi	0.001
HI_native	US_lab	0.001

¹Europe: Italy, France, Slovenia, Switzerland, and Spain; US_wild sites: New York and California; US_lab sites: New York and California; HI_immigrans: *D. immgrans* caught in Hawai'i; HI_native: native Hawaiian *Drosophilia*.

would contain different communities and more closely resemble those of local drosophilids. Alternatively, successful colonization could be aided by a core microbiome that is maintained regardless of host location. Our analysis of *D. suzukii* microbiomes collected from three continents and two islands provides evidence for both of these scenarios. While these results identify compositional trends rather than functional roles, they establish a valuable foundation for future experiments to test how microbiome variation influences colonization and host physiology.

²Outcomes from Wilcoxon Rank Sum tests; *p*-values < 0.05 in bold.

²Outcomes from PERMANOVA; p-values < 0.05 in bold.



Bacterial and fungal community profiles for native Hawaiian *Drosophila*, *D. immigrans*, and *D. suzukii* flies collected from Moloka'i, Lana'i, and Hawai'i islands. Outcomes of statistical comparisons are detailed in Table 3. **(A)** Alpha-diversity analyses based on ASVs reveal no significant differences in bacterial profiles. Each point represents a single fly. **(B)** Non-metric multidimensional scaling (NMDS) plot depicting Bray-Curtis dissimilarity distances; ANOSIM: p = 0.003, R = 0.18. Each point represents a single fly. Populations are compared at the family level. Ellipses represent 95% confidence intervals. **(C)** Relative abundance plots indicating the 10 most prevalent bacterial families found between the three populations; *taxa that differed significantly (f-test, p < 0.0001). **(D)** Alpha-diversity analyses based on ASVs reveal no significant differences in fungal profiles. **(E)** NMDS plot depicting Bray-Curtis dissimilarity distances; ANOSIM: p = 0.01, R = 0.12. Ellipses represent 95% confidence intervals. **(F)** Relative abundance plots showing the 10 most prevalent fungal families common to the three populations. There were no significant differences in relative abundances (f-test, p > 0.05). **(G)** Venn diagram based on the 10 most abundant taxa for each population showing bacterial families common to each of the Hawaiii populations; for all 16S rRNA analyses, native Hawaiian *Drosophila*, n = 128, *D. immigrans*, n = 27, *D. suzukii*, n = 9. **(H)** Venn diagram based on the 10 most abundant taxa for each population showing overlapping fungal families; native Hawaiian *Drosophila*; for all ITS analyses n = 129, *D. immigrans*, n = 28, *D. suzukii*, n = 9.

Multi-region trends and local influences on the *D. suzukii* bacterial microbiome

Wild populations from each of the major sites exhibited distinct compositional differences, indicating geographically structured variation in microbiome composition. However, three of the seven families present in all wild *D. suzukii, Acetobacteraceae, Erwiniaceae*, and *Pseudomonadaceae*, were also found in a recent survey of wild *D. suzukii* populations from Oregon (USA) and Missouri (USA) (Bhandari et al., 2025), consistent with the possibility that taxa from these families form stable, mutualistic

associations with *D. suzukii*. Two of the *D. suzukii*-associated bacterial families have species members with sugar production and cellulose degradation activities, and may facilitate *D. suzukii's* ability to use multiple host fruits (Gao et al., 2023; Netrusov et al., 2023; Wünsche and Schmid, 2023; López-Hernández et al., 2025). Both *Acetobacteraceae* and *Lactobacillaceae* are considered facultative members of the *D. melanogaster* microbiome that promote host growth and participate in nutritional mutualism (Storelli et al., 2011; Pais et al., 2018). The *Erwiniaceae* family is also found in another widespread invasive insect, ambrosia beetles, for which it provides nutritional support and antibiotic protection

TABLE 3 *P-value* outcomes of pairwise alpha- and beta-diversity comparisons of family-level bacterial (top) and fungal (bottom) community profiles from Hawai'i populations shown in Figure 2.

Target gene	Group 1	Group 2	Alpha-diversity ¹		Beta-diversity ²
			Chao1	Shannon	beta-diversity
16S rRNA	D. immigrans	Hawaiian <i>Drosophila</i>	0.001	0.250	0.072
	D. suzukii	Hawaiian <i>Drosophila</i>	0.008	0.113	0.001
	D. suzukii	D. immigrans	0.858	0.250	0.001
ITS	D. immigrans	Hawaiian <i>Drosophila</i>	0.686	0.791	0.093
	D. suzukii	Hawaiian <i>Drosophila</i>	0.210	0.680	0.057
	D. suzukii	D. immigrans	0.339	0.680	0.145

¹Outcomes from Wilcoxon Rank Sum tests; bold values indicate statistical significance at the p < 0.05 level.

(Cambronero-Heinrichs et al., 2023). The incorporation of bacterial taxa that offer enhanced metabolic capabilities is a common strategy observed in multiple invasive host species. Understanding the functional contributions of these microbes to *D. suzukii* adaptation may identify novel strategies for population control (Hamby and Becher, 2016).

Comparing the microbiomes of invasive species to native Hawaiian species

Although D. suzukii in Hawai'i share features of their microbial profile with populations from other regions, their microbiome composition more closely resembles that of other Hawaiian drosophilids. This outcome indicates that D. suzukii populations may both retain a subset of widespread bacterial families regardless of area of occurrence, yet enrich for other groups of local bacteria when colonizing a new habitat. For example, the Rhizobiaceae family, which appears to be enriched only in Hawai'i D. suzukii, belong to the Bacteroidetes phyla, members of which are capable of degrading simple and complex polysaccharidess (Vera-Ponce de León et al., 2020; Nweze et al., 2024). At the level of genus, two taxa appear to be enriched in Hawai'i D. suzukii: Zymobacter and Citrobacte, both of which are known to confer beneficial properties to host insects. Zymobacter facilitates sugar fermentation and is relatively abundant in fieldcollected mosquitoes and stingless bees (Hegde et al., 2018; Hall et al., 2020). In addition, Citrobacter provides resistances to insecticide and enhances development in black soldier flies (Cheng et al., 2017; Luo et al., 2023). Incorporation of microbes that potentially enhance metabolic capabilities may allow D. suzukii to expand its ecological niche. These associations may reflect conserved adaptation strategies in addition to widespread and consistent opportunistic colonization. Future studies of native vs. invasive flies from other sites are needed to determine whether this is a general strategy. Additionally, measurements of host range and adaptation paired with experimental manipulation of the microbiome will directly address the hypothesis that local microbe incorporation is a necessary step for successful colonization.

D. immigrans is considered a member of the guild of cosmopolitan Drosophila species, found worldwide (Nunney,

1996). Notably, the microbiome of *D. immigrans*, first reported in Hawai'i in 1948 (Mainland, 1949), more closely resembles that of endemic Hawaiian flies than *D. suzukii*, a species that arrived only in 1980 (Hauser, 2011). The extended establishment time of *D. immigrans* in Hawai'i compared to *D. suzukii* may have allowed the former to assimilate more of the local microbes. The mycobiome communities of invasive vs. native flies in the Hawaiian Island also exhibit similar compositional profiles. Given that flies obtain much of their microbiome through diet and environment interactions rather than vertical transmission (Douglas, 2019), the general overlap in fungal composition may reflect shared habitats among the native and invasive drosophilids in Hawai'i (Kaneshiro, 1983; Magnacca et al., 2008; Leblanc et al., 2009).

Overall, our findings reveal both geographic differentiation and partial overlap in D. suzukii microbiomes across continents and the Hawaiian Islands. These patterns are consistent with a core microbiome retained across regions and with enrichment of locally prevalent microbes. These results also suggest that plasticity in the D. suzukii microbiome may facilitate this species' rapid colonization of novel ecological niches. Similar to a previous study of invasive Siganus fish in the Mediterranean Sea (Escalas et al., 2022), we identified a shift in microbiome composition when comparing D. suzukii from the native range in Asia to invaded ranges. Whether compositional change provides adaptive advantages (e.g., expanding dietary resources) remains an open question. Further functional exploration of how microbes contribute to host physiology and local adaptation through, for example, common garden transplant experiments with native vs. invasive hosts may lead to the development of new microbiome methods for population control. Incorporating microbiome manipulations and metagenomic analyses into invasion ecology could also clarify whether microbes act as opportunistic colonizers or facilitators of ecological expansion.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/, PRJNA1270093

 $^{^2}$ Outcomes from PERMANOVA; bold values indicate statistical significance at the p < 0.05 level.

https://www.ncbi.nlm.nih.gov/, PRJEB50289 https://www.ncbi.nlm.nih.gov/, PRJNA412893 https://www.ncbi.nlm.nih.gov/, PRJNA347319 https://www.ncbi.nlm.nih.gov/, PRJNA719706.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. AB: Conceptualization, Data curation, Formal Analysis, Methodology, Writing – original draft, Writing – review & editing. DP: Conceptualization, Resources, Writing – original draft, Writing – review & editing. JY: Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Supplementary material

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References

Adrion, J. R., Kousathanas, A., Pascual, M., Burrack, H. J., Haddad, N. M., Bergland, A. O., et al. (2014). Drosophila suzukii: the genetic footprint of a recent, worldwide invasion. *Mol. Biol. Evol.* 31, 3148–3163. doi: 10.1093/molbev/msu246

Andreazza, F., Bernardi, D., dos Santos, R. S. S., Garcia, F. R. M., Oliveira, E. E., Botton, M., et al. (2017). Drosophila suzukii in Southern Neotropical region: current status and future perspectives. *Neotropical Entomology* 46, 591–605. doi: 10.1007/s13744-017-0554-7

Arisdakessian, C., Cleveland, S. B., and Belcaid, M. (2020). "MetaFlow|mics: Scalable and reproducible nextflow pipelines for the analysis of microbiome marker data," in

Practice and Experience in Advanced Research Computing (PEARC '20). (New York, NY, USA: Association for Computing Machinery).

Bhandari, R., Wong, A.-N., Lee, J. C., Boyd, A., Shelby, K., Ringbauer, J. Jr., et al. (2025). Microbiome composition and co-occurrence dynamics in wild Drosophila suzukii are influenced by host crop, fly sex, and sampling location. *Microbiol. Spectr.* 13, e0260824. doi: 10.1128/spectrum.02608-24

Bing, X., Gerlach, J., Loeb, G., and Buchon, N. (2018). Nutrient-dependent impact of microbes on Drosophila suzukii development. *mBio* 9, e02199-17. doi: 10.1128/mBio.02199-17

Bolda, M. P., Goodhue, R., and Zalom, F. (2010). Spotted wing drosophila: potential economic impact of a newly established pest. *Giannini Foundation Agric. Econ* 13, 5–8.

Calabria, G., Máca, J., Bächli, G., Serra, L., and Pascual, M. (2012). First records of the potential pest species Drosophila suzukii (Diptera: Drosophilidae) in Europe. *J. Appl. Entomology* 136, 139–147. doi: 10.1111/j.1439-0418.2010.01583.x

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J., and Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nat. Methods* 13, 581–583. doi: 10.1038/nmeth.3869

Cambronero-Heinrichs, J. C., Battisti, A., Biedermann, P. H. W., Cavaletto, G., Castro-Gutierrez, V., Favaro, L., et al. (2023). Erwiniaceae bacteria play defensive and nutritional roles in two widespread ambrosia beetles. FEMS Microbiol. Ecol. 99, fiad144. doi: 10.1093/femsec/fiad144

Chandler, J. A., Lang, J. M., Bhatnagar, S., Eisen, J. A., and Kopp, A. (2011). Bacterial communities of diverse Drosophila species: ecological context of a host-microbe model system. *PLoS Genet.* 7, e1002272. doi: 10.1371/journal.pgen.1002272

Cheng, D., Guo, Z., Riegler, M., Xi, Z., Liang, G., and Xu, Y. (2017). Gut symbiont enhances insecticide resistance in a significant pest, the oriental fruit fly Bactrocera dorsalis (Hendel). *Microbiome* 5, 13. doi: 10.1186/s40168-017-0236-z

Chevalier, C., Stojanović, O., Colin Didier, J., Suarez-Zamorano, N., Tarallo, V., Veyrat-Durebex, C., et al. (2015). Gut microbiota orchestrates energy homeostasis during cold. *Cell* 163, 1360–1374. doi: 10.1016/j.cell.2015.11.004

Cini, A., Ioriatti, C., and Anfora, G. (2012). A review of the invasion of Drosophila suzukii in Europe and a draft research agenda for integrated pest management. *Bull. Insectol.* 65, 149–160.

Curbelo, K., Price, D. K., and Koch, J. B. (2022). Brief assessment of Drosophila suzukii (Diptera: Drosophilidae) abundance in forest and non-forested habitats across an altitude gradient on Mauna Loa, Hawaiʻi. *Pac Sci.* 75, 513–524. doi: 10.2984/75.4.4

Deprá, M., Poppe, J. L., Schmitz, H. J., De Toni, D. C., and Valente, V. L. S. (2014). The first records of the invasive pest Drosophila suzukii in the South American continent. *J. Pest Sci.* 87, 379–383. doi: 10.1007/s10340-014-0591-5

Douglas, A. E. (2019). Simple animal models for microbiome research. Nat. Rev. Microbiol. 17, 764–775. doi: 10.1038/s41579-019-0242-1

Escalas, A., Auguet, J. C., Avouac, A., Belmaker, J., Dailianis, T., Kiflawi, M., et al. (2022). Shift and homogenization of gut microbiome during invasion in marine fishes. *Anim. Microbiome* 4, 37. doi: 10.1186/s42523-022-00181-0

Feng, S., DeGrey, S. P., Guédot, C., Schoville, S. D., and Pool, J. E. (2024). Genomic diversity illuminates the environmental adaptation of Drosophila suzukii. *Genome Biol. Evol.* 16, evae195. doi: 10.1093/gbe/evae195

Fountain, M. T., Bennett, J., Cobo-Medina, M., Conde Ruiz, R., Deakin, G., Delgado, A., et al. (2018). Alimentary microbes of winter-form Drosophila suzukii. *Insect Mol. Biol.* 27, 383–392. doi: 10.1111/imb.12377

Gao, H. H., Zhao, S., Wang, R. J., Qin, D. Y., Chen, P., Zhang, A. S., et al. (2023). Gut bacterium promotes host fitness in special ecological niche by affecting sugar metabolism in Drosophila suzukii. *Insect Sci.* 30, 1713–1733. doi: 10.1111/1744-7917.13189

Hall, M. A., Brettell, L. E., Liu, H., Nacko, S., Spooner-Hart, R., Riegler, M., et al. (2020). Temporal changes in the microbiome of stingless bee foragers following colony relocation. *FEMS Microbiol. Ecol.* 97, fiaa236. doi: 10.1093/femsec/fiaa236

Hamby, K. A., and Becher, P. G. (2016). Current knowledge of interactions between Drosophila suzukii and microbes, and their potential utility for pest management. *J. Pest Sci.* 89, 621–630. doi: 10.1007/s10340-016-0768-1

Hauser, M. (2011). A historic account of the invasion of Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. *Pest Manag Sci.* 67, 1352–1357. doi: 10.1002/ps.2265

Hegde, S., Khanipov, K., Albayrak, L., Golovko, G., Pimenova, M., Saldaña, M. A., et al. (2018). Microbiome Interaction Networks and Community Structure From Laboratory-Reared and Field-Collected Aedes aEgypti, Aedes albopictus, and Culex quinquefasciatus Mosquito Vectors. *Front. Microbiol.* 9. doi: 10.3389/fmicb.2018.02160

Houwenhuyse, S., Stoks, R., Mukherjee, S., and Decaestecker, E. (2021). Locally adapted gut microbiomes mediate host stress tolerance. *ISME J.* 15, 2401–2414. doi: 10.1038/s41396-021-00940-y

Jiménez-Padilla, Y., Esan, E. O., Floate, K. D., and Sinclair, B. J. (2020). Persistence of diet effects on the microbiota of Drosophila suzukii (Diptera: Drosophilidae). *Can. Entomol* 152, 516–531. doi: 10.4039/tce.2020.37

Kaneshiro, K. Y. (1983). Drosophila (Sophophora) suzukii (Matsumura). *Proc. Hawaiian Entomol Soc.* 24, 179.

Kanzawa, T. (1939). Studies on Drosophila suzukii Mats. Kofu, Yamanashi Agric. Exp. Sta. 49. Rev App Ent. 29, 622.

Koch, J. B., Dupuis, J. R., Jardeleza, M.-K., Ouedraogo, N., Geib, S. M., Follett, P. A., et al. (2020). Population genomic and phenotype diversity of invasive Drosophila suzukii in Hawai'i. *Biol. Invasions* 22, 1753–1770. doi: 10.1007/s10530-020-02217-5

Kohl, K. D., Weiss, R. B., Cox, J., Dale, C., and Dearing, M. D. (2014). Gut microbes of mammalian herbivores facilitate intake of plant toxins. *Ecol. Lett.* 17, 1238–1246. doi: 10.1111/ele.12329

Koštál, V., Korbelová, J., Štětina, T., Poupardin, R., Colinet, H., Zahradníčková, H., et al. (2016). Physiological basis for low-temperature survival and storage of quiescent

larvae of the fruit fly Drosophila melanogaster. Sci. Rep. 6, 32346. doi: 10.1038/srep32346

Kwadha, C. A., Okwaro, L. A., Kleman, I., Rehermann, G., Revadi, S., Ndlela, S., et al. (2021). Detection of the spotted wing drosophila, Drosophila suzukii, in continental sub-Saharan Africa. *J. Pest Sci.* 94, 251–259. doi: 10.1007/s10340-021-01330-1

Leblanc, L., O'Grady, P., Rubinoff, D., and Montgomery, S. (2009). New immigrant drosophilidae in Hawaii, and a checklist of the established immigrant species. *Proc. Hawaiian Entomol Soc.* 41, 121–127.

Lin, Q., Zhai, Y., Chen, H., Qin, D., Zheng, L., and Gao, H. (2021). Analyses of the gut bacteriomes of four important Drosophila pests. *Can. Entomologist* 153, 757–773. doi: 10.4039/tce.2021.45

Little, C. M., Chapman, T. W., and Hillier, N. K. (2020). Plasticity is key to success of Drosophila suzukii (Diptera: Drosophilidae) invasion. *J. Insect Sci.* 20, 5. doi: 10.1093/iisesa/jeaa034

Liu, G., Zheng, X., Long, H., Rao, Z., Cao, L., and Han, R. (2021). Gut bacterial and fungal communities of the wild and laboratory-reared thitarodes larvae, host of the Chinese medicinal fungus Ophiocordyceps sinensis on Tibetan Plateau. *Insects* 12, 5. doi: 10.3390/insects12040327

López-Hernández, M. G., Rincón-Rosales, R., Rincón-Molina, C. I., Manzano-Gómez, L. A., Gen-Jiménez, A., Maldonado-Gómez, J. C., et al. (2025). Diversity and functional potential of gut bacteria associated with the insect Arsenura armida (Lepidoptera: Saturniidae). *Insects* 16, 711. doi: 10.3390/insects16070711

Luo, X., Fang, G., Chen, K., Song, Y., Lu, T., Tomberlin Jeffery, K., et al. (2023). A gut commensal bacterium promotes black soldier fly larval growth and development partly via modulation of intestinal protein metabolism. $mBio\ 14$, e01174–e01123. doi: 10.1128/mbio.01174-23

Magnacca, K. N., Foote, D., and O'Grady, P. M. (2008). A review of the endemic Hawaiian Drosophilidae and their host plants. *Zootaxa* 1728, 1–58. doi: 10.11646/zootaxa.1728.1.1

Mainland, G. B. (1949). Note on new drosophilids. *Proc. Hawaiian Entomol Soc.* 13, 326–327.

Martinez-Sañudo, I., Simonato, M., Squartini, A., Mori, N., Marri, L., and Mazzon, L. (2018). Metagenomic analysis reveals changes of the Drosophila suzukii microbiota in the newly colonized regions. *Insect Sci.* 25, 833–846. doi: 10.1111/1744-7917.12458

McMurdie, P. J., and Holmes, S. (2013). phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. *PloS One* 8, e61217. doi: 10.1371/journal.pone.0061217

Medeiros, M. J., Schoville, S., Price, D., and Yew, J. Y. (2025). Abiotic factors are the primary determinants of endemic Hawaiian Drosophila microbiome assembly. *bioRxiv*. doi: 10.1101/2025.05.06.652154

Medeiros, M. J., Seo, L., Macias, A., Price, D. K., and Yew, J. Y. (2024). Bacterial and fungal components of the microbiome have distinct roles in Hawaiian Drosophila reproduction. *ISME Comm* 4, ycae134. doi: 10.1093/ismeco/ycae134

Mérel, V., Gibert, P., Buch, I., Rodriguez Rada, V., Estoup, A., Gautier, M., et al. (2021). The worldwide invasion of Drosophila suzukii is accompanied by a large increase of transposable element load and a small number of putatively adaptive insertions. *Mol. Biol. Evol.* 38, 4252–4267. doi: 10.1093/molbev/msab155

Mueller, U. G., Mikheyev, A. S., Hong, E., Sen, R., Warren, D. L., Solomon, S. E., et al. (2011). Evolution of cold-tolerant fungal symbionts permits winter fungiculture by leafcutter ants at the northern frontier of a tropical ant–fungus symbiosis. *Proc. Natl. Acad. Sci. U.S.A.* 108, 4053. doi: 10.1073/pnas.1015806108

Naranjo-Lázaro, J. M., Mellín-Rosas, M. A., González-Padilla, V. D., Sánchez-González, J. A., Moreno-Carrillo, G., and Arredondo-Bernal, H. C. (2014). Susceptibility of Drosophila suzukii matsumura (Diptera: Drosophilidae) to entomophatogenic fungi. Southwestern Entomologist 39, 201–203. doi: 10.3958/059.039.0119

Netrusov, A. I., Liyaskina, E. V., Kurgaeva, I. V., Liyaskina, A. U., Yang, G., and Revin, V. V. (2023). Exopolysaccharides producing bacteria: A review. *Microorganisms* 11, 1541. doi: 10.3390/microorganisms11061541

Nilsson, R. H., Larsson, K. H., Taylor, A. F. S., Bengtsson-Palme, J., Jeppesen, T. S., Schigel, D., et al. (2019). The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* 47, D259–d264. doi: 10.1093/nar/gky1022

Nunney, L. (1996). The colonization of organges by the cosmopolitan Drosophila. Oecologia~108, 552-561.~doi:~10.1007/bf00333733

Nweze, J. E., Šustr, V., Brune, A., and Angel, R. (2024). Functional similarity, despite taxonomical divergence in the millipede gut microbiota, points to a common trophic strategy. *Microbiome* 12, 16. doi: 10.1186/s40168-023-01731-7

Pais, I. S., Valente, R. S., Sporniak, M., and Teixeira, L. (2018). Drosophila melanogaster establishes a species-specific mutualistic interaction with stable gut-colonizing bacteria. *PloS Biol.* 16, e2005710. doi: 10.1371/journal.pbio.2005710

Parada, A. E., Needham, D. M., and Fuhrman, J. A. (2016). Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. *Environ. Microbiol.* 18, 1403–1414. doi: 10.1111/1462-2920.13023

Poyet, M., Le Roux, V., Gibert, P., Meirland, A., Prévost, G., Eslin, P., et al. (2015). The wide potential trophic niche of the Asiatic fruit fly Drosophila suzukii: the key of its

invasion success in temperate Europe? PloS One 10, e0142785. doi: 10.1371/journal.pone.0142785

Price, D. K., West, K., Cevallos-Zea, M., Cahan, S. H., Nunez, J. C. B., Longman, E. K., et al. (2025). Microbiome composition shapes temperature tolerance in a Hawaiian picture-winged Drosophila. *J. Exp. Biol.* 228, 1-14. doi: 10.1242/jeb.250973

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., et al. (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.* 41, D590–D596. doi: 10.1093/nar/gks1219

R Core Team (2022). R: A language and environment for statistical computing (Vienna, Austria: R.F.f.S. Computing).

Robert, V., Vu, D., Amor, A. B., van de Wiele, N., Brouwer, C., Jabas, B., et al. (2013). MycoBank gearing up for new horizons. *IMA Fungus* 4, 371–379. doi: 10.5598/imafungus.2013.04.02.16

Sánchez-Ramos, I., Fernández, C. E., and González-Núñez, M. (2019a). Comparative analysis of thermal performance models describing the effect of temperature on the preimaginal development of Drosophila suzukii. *J. Pest Sci.* 92, 523–541. doi: 10.1007/s10340-018-1030-9

Sánchez-Ramos, I., Gómez-Casado, E., Fernández, C. E., and González-Núñez, M. (2019b). Reproductive potential and population increase of Drosophila suzukii at constant temperatures. *Entomologia Generalis* 39, 103-115. doi: 10.1127/entomologia/2019/0794

Shik, J. Z., and Dussutour, A. (2020). Nutritional dimensions of invasive success. Trends Ecol. Evol. 35, 691–703. doi: 10.1016/j.tree.2020.03.009

Shu, R., Hahn, D. A., Jurkevitch, E., Liburd, O. E., Yuval, B., and Wong, A. C.-N. (2021). Sex-dependent effects of the microbiome on foraging and locomotion in Drosophila suzukii. *Front. Microbiol.* 12. doi: 10.3389/fmicb.2021.656406

Staubach, F., Baines, J. F., Kunzel, S., Bik, E. M., and Petrov, D. A. (2013). Host species and environmental effects on bacterial communities associated with Drosophila in the laboratory and in the natural environment. *PLoS One* 8, e70749. doi: 10.1371/journal.pone.0070749

Storelli, G., Defaye, A., Erkosar, B., Hols, P., Royet, J., and Leulier, F. (2011). Lactobacillus plantarum promotes Drosophila systemic growth by modulating hormonasignals through TOR-dependent nutrient sensing. *Cell Metab.* 14, 403–414. doi: 10.1016/j.cmet.2011.07.012

Tait, G., Mermer, S., Stockton, D., Lee, J., Avosani, S., Abrieux, A., et al. (2021). Drosophila suzukii (Diptera: Drosophilidae): A decade of research towards a sustainable integrated pest management program. *J. Econ Entomol* 114, 1950–1974. doi: 10.1093/ice/toab158

Tefit, M. A., Budiman, T., Dupriest, A., and Yew, J. Y. (2023). Environmental microbes promote phenotypic plasticity in reproduction and sleep behaviour. *Mol. Ecol.* 32, 5186–5200. doi: 10.1111/mec.17095

Vera-Ponce de León, A., Jahnes, B. C., Duan, J., Camuy-Vélez, L. A., and Sabree, Z. L. (2020). Cultivable, host-specific bacteroidetes symbionts exhibit diverse polysaccharolytic strategies. *Appl. Environ. Microbiol.* 86, e00091-20. doi: 10.1128/aem.00091-20

White, T. J., Bruns, T., Lee, S., and Taylor, J. W. (1990). "Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics," in *PCR protocols: a guide to methods and applications*. Eds. M. A. Innis, D. H. Gelfand, J. J. Sninsky and T. J. White (Academic Press, Inc, New York, NY), 315–322.

Wünsche, J., and Schmid, J. (2023). Acetobacteraceae as exopolysaccharide producers: Current state of knowledge and further perspectives. *Front. Bioeng Biotechnol.* 11. doi: 10.3389/fbioe.2023.1166618

Yamada, R., Deshpande, S. A., Bruce, K. D., Mak, E. M., and Ja, W. W. (2015). Microbes promote amino acid harvest to rescue undernutrition in Drosophila. *Cell Rep.* 10, 865–872. doi: 10.1016/j.celrep.2015.01.018

Yilmaz, P., Parfrey, L. W., Yarza, P., Gerken, J., Pruesse, E., Quast, C., et al. (2014). The SILVA and "All-species Living Tree Project (LTP)" taxonomic frameworks. *Nucleic Acids Res.* 42, D643–D648. doi: 10.1093/nar/gkt1209

Zhang, S., Song, F., Wang, J., Li, X., Zhang, Y., Zhou, W., et al. (2024). Gut microbiota facilitate adaptation of invasive moths to new host plants. *ISME J.* 18, wrae031. doi: 10.1093/ismejo/wrae031