First record of the invasive pest *Drosophila suzukii* in Ukraine indicates multiple sources of invasion

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**Abstract** *Drosophila suzukii*, commonly known as the spotted-wing *Drosophila*, is an invasive polyphagous fruit pest, which has emerged as a global threat to agriculture in the Americas and in Europe. Due to the rapid spread, great economic losses and its pest behavior, *D. suzukii* represents a powerful model for invasion biology and pest management studies. However, its current European distribution, invasion routes and levels of genetic diversity in populations of *D. suzukii* are poorly understood. We present the first report of *D. suzukii* from Ukraine, with the invasion likely occurring close to 2014. The pattern of genetic variation at *cytochrome oxidase I* among *D. suzukii* populations from Europe, USA and Asia reveals comparatively high genetic diversity in the Ukrainian population of this pest species, suggesting a complex invasion scenario from multiple sources. Further monitoring patterns of genetic variation across space and time, to better understand the invasion routes of this invasive insect pest, will be an essential part for developing successful pest management strategies.

**Keywords** Invasive species · Spotted-wing *Drosophila* · Population genetics

**Key message**

- *Drosophila suzukii* is an invasive agricultural pest that has been expanding its range since the late 2000s.
- Our data represent the genetic pattern at the start of an invasion by *D. suzukii* in Ukraine.
- *COI* sequence data reveal high genetic diversity in the Ukrainian *D. suzukii* population.
- Our study indicates the potential for multiple sources of *D. suzukii* invasion into Europe, along with possible recurrent introductions.

**Introduction**

Invasive species represent significant threats to biodiversity, with impacts on non-native habitats potentially having deleterious ecosystem effects (Gurevitch and Padilla 2004) and strong economic burden (Pimentel et al. 2005). *Drosophila suzukii* (Matsumura, 1931), also known as the spotted-wing *Drosophila* (SWD), is an invasive, destructive fruit crop pest, which represents a prominent example of one of the most severe ongoing biological invasions of the Western Hemisphere (Asplen et al. 2015).

Most drosophilids attack overripe, rotten or damaged fruits and generally are not considered as pests. Differently, *D. suzukii* is one of the very few drosophilids that can
oviposit in healthy, ripe fruits, and thus, this species can cause considerable damage to crops (Mitsui et al. 2006; Lee et al. 2011). As a consequence, the SWD is one of the most damaging pests of cultivated soft-skinned tree fruits and berry crops in temperate regions (Saguez et al. 2013). Indeed, within the USA, the estimated annual economic losses attributed to crop damage by D. suzukii are in the order of $700 million (Walsh et al. 2011; Wiman et al. 2016). The fast-paced global spread of D. suzukii, accompanied with a severe economic burden, highlights the importance of tracing current distribution and invasion routes of this species.

SWD is native to Asia (Kanzawa 1939; Calabria et al. 2012) but, by 2008, invasions by D. suzukii were reported in both the USA (California) (Hauser et al. 2009) and in Western Europe (Spain) (Calabria et al. 2012). Since 2008, D. suzukii has expanded its introduced range quite rapidly becoming a key pest species throughout the Americas (Hauser 2011; Deprá et al. 2014; Wang et al. 2016) and in Europe (Cini et al. 2012; Asplén et al. 2015; Arnó et al. 2016). Despite the simultaneous occurrence of invasions by D. suzukii into North America and Europe, genetic data indicate that these invasions were independent events (Adrion et al. 2014). Levels of genetic diversity in North American populations of D. suzukii are quite high, but are relatively low in Europe (and also the Hawaiian Islands) (Adrion et al. 2014). This comparatively low genetic diversity of European D. suzukii is hypothesized to be a consequence of a bottleneck, yet this idea is based on data from only one European population in Spain (Adrion et al. 2014). Subsequent genetic data that used a large (n = 28) panel of microsatellite loci showed similar polymorphism but strong genetic differentiation between a population from France and a population from Hawaii, consistent with the pattern described above (Frajmout et al. 2015). Despite the wealth of available genomic data for the SWD (Chiu et al. 2013; Ramasamy et al. 2016) and the research efforts in many other fields of D. suzukii biology (Hamby et al. 2016), it is still inconclusive whether European D. suzukii populations are generally characterized by low genetic diversity. The possibility of independent, multiple and recurrent introductions in different populations highlights the need for gathering more genetic data through space and time.

Furthermore, understanding the level of genetic variation in natural populations of D. suzukii has a particular importance from the perspective of developing successful global pest management strategies (Haye et al. 2016), as genetic diversity often positively correlates with adaptive potential (Reed and Frankham 2003; Barrett and Schluter 2008). Moreover, genetic diversity could inform on the size and number of independent and/or recurrent introductions that could be occurring and, thus, should be considered for appropriate management actions.

Although D. suzukii is the only species of the ‘me- lanogaster’ group in Europe that is characterized by (1) a large, pointed and serrated ovipositor in the females, and (2) by a dark spot near the wing tips of adult males, these characters do not allow unambiguous morphological identification during biodiversity surveys by non-specialists. For example, the conspicuous male wing spots require up to 2 days to fully develop, and large serrated ovipositor is similar to that of females of closely related species such as Drosophila subpulchrella (Hauser 2011). Finally, the immature stages cannot be identified by their morphology. Thus, there is a need to support surveys of Drosophila species with genetic data to provide unambiguous confirmation of the identity of any suspected D. suzukii (Murphy et al. 2016). One of the most widely used molecular methods for identifying D. suzukii is through DNA barcoding: sequence analysis of a fragment of the mitochondrial cytochrome oxidase I (COI) gene (Hebert et al. 2003; Hauser 2011).

We report (1) the first record of D. suzukii from Ukraine, but only in the most southern locality that was sampled (Yalta, Crimea) and (2) COI gene sequence data that, by comparison with sequenced data available from public databases, indicate high genetic diversity of D. suzukii in Ukraine that points to a complex invasion scenario, potentially from multiple sources. Our study sets the baseline of presence/absence data of this species for invasion of Ukraine, which may contribute to further monitoring studies of this invasive pest species and to understand its dispersal behavior.

### Materials and methods

#### Sample collection

Specimens of D. suzukii were found during biodiversity surveys for Drosophila species that were undertaken in the summer–autumn seasons of 2014 and 2015. The seven sampling sites throughout Ukraine were: Yalta, Odesa, Uman’, Kharkiv, Piryatin, Kyiv and Chornobil (Fig. 1). Most of Ukraine has a humid continental climate, except for southern Crimea (i.e., the Yalta sample location), which is subtropical (Köppen 1931; Kottek et al. 2006). Brief descriptions of the study sites are given in Sergy et al. (2015), with the only difference being the sample site in Yalta, where sampling during 2014–2015 was performed in a private garden in Yalta city center that had mixed vegetation, fig tree (Ficus carica) and raspberry (Rubus idaeus) nearby.

At each locality, flies were netted over four traps that had been baited with 6–7 smashed fermented apples and about 300 ml of commercially available wheat beer (Sergy et al. 2015). The traps that consisted of thick plastic bags of different colors, separated by 5–10 m, were kept at each location for 72 h. Captured flies were identified on the

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basis of their external morphology under a 7×45× stereomicroscope (Konus Crystal, Italy). Morphological identification of D. suzukii was carried out according to Hauser (2011). Unfortunately, surveys in 2014 were not preserved properly and D. suzukii specimens from 2014 in Yalta (Crimea) could not be used for molecular analysis. Given the relevance of finding D. suzukii in Ukraine, we performed sampling in the same location in Yalta during two trapping periods in 2015, with subsequent SWD individuals’ preservation in 96% ethanol at −20 °C for the downstream molecular analyses.

Molecular methods

Genomic DNA was extracted from nine individuals of D. suzukii (sampled during summer 2015) using a high salt protocol, modified from Aljanabi and Martinez (1997). A 693-bp fragment of the COI mtDNA gene was amplified using the universal primers LCO1490 and HCO2198 (Folmer et al. 1994). Polymerase chain reactions (PCR) were performed in 10 μL reactions containing 2 μL of DNA, 5 μL of 2× DreamTaq Green PCR Master Mix (Thermo Scientific) and 0.5 μM of both forward and reverse primers. Amplification conditions were: 95 °C for 3 min, then 35 cycles of: 95 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by 72 °C for 7 min. For sequencing, the PCR products were purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Thermo Scientific), cycle-sequenced in both directions using BigDye v.3.1 chemistry (Applied Biosystems) and visualized with an ABI3730 (Applied Biosystems). Sequences were edited manually with BioEdit v.7.2.5 (Hall 1999) and aligned and then translated to confirm the absence of stop codons with MEGA6 (Tamura et al. 2013). All D. suzukii sequences were deposited in GenBank (accession numbers: KX268719-KX268727).

To infer the genetic relationships of these Ukrainian D. suzukii with native (Asian) and invasive (European and USA) populations of D. suzukii, all available COI gene sequences for D. suzukii were downloaded from GenBank. Subsequently, we only used those COI sequences that (1) corresponded to the same fragment that we had sequenced and (2) whose GenBank record contained unambiguous information about the sampling location. This provided us
with 74 sequences of the SWD from Europe (Portugal, Spain, Italy and Serbia), USA (California, Oregon, Washington and Arkansas), China and Japan (for details, see Electronic Supplementary Material 1). A haplotype network of these sequences was constructed with TCS v.1.21 (Clement et al. 2000) and edited using tcsBU (TCS Beautifier) (Múrias Dos Santos et al. 2016).

Results

Individuals of Drosophila genus were collected from seven regions throughout Ukraine, between 2014 and 2015, and identified as 14 different Drosophila species (Table 1). The Drosophilidae species fauna of Ukraine is quite typical for the Palearctic region (Bächli and Rocha-Pite 1982). D. suzukii was collected during August on both sampling years from Yalta (Crimea) (Table 1), which represents the first record of D. suzukii in Ukraine.

Sequences of COI for nine individuals from Yalta (collected in 2015) included four different haplotypes. The nine sequences were aligned with data from 74 additional D. suzukii COI sequences derived from GenBank from Asia, Europe and USA (accession numbers are given in Electronic Supplementary Material 1). The final alignment consisted of a 606-bp fragment of the COI gene (available in Electronic Supplementary Material 2). Overall, 23 different haplotypes were found and the network reconstruction uncovered substantial genetic diversity in the SWD, most of which was derived from samples of D. suzukii from its putative native range in Japan (Fig. 2). With regard to invasion biology, it is notable that more COI haplotypes were found in the D. suzukii samples from Ukraine than all other European countries for which genetic data are available (n = 3 haplotypes in total) (Fig. 2). The most common European D. suzukii haplotype was present in D. suzukii samples from Ukraine, as well as in the samples from Japan, but not in the D. suzukii samples from USA. This haplotype was found in all other European countries for which genetic data were reported. High levels of diversity in Ukrainian and the USA D. suzukii populations are comparable, and Ukrainian D. suzukii shared COI haplotypes with D. suzukii samples from the USA, and both regions share haplotypes with D. suzukii from Japan and China (Fig. 2). Thus, Ukrainian D. suzukii population has genetic similarities to European and the USA invasion foci. Finally, we note that two additional haplotypes were found in Europe, a private haplotype in the D. suzukii samples from Italy and one haplotype from Serbia, which was also found in samples from the USA and China (Fig. 2), but not other European locations (including Ukraine). One additional shared haplotype was found in the USA and China, while the remaining haplotypes were only reported from Japan.

Discussion

Drosophila suzukii is native to mountainous temperate regions of eastern Asia (Kanzawa 1939; Asplen et al. 2015) and has likely dispersed to Western countries via trade of fruit by sea (Hauser 2011; Calabria et al. 2012). Invasion by D. suzukii presents a major agricultural problem, and identifying the routes of invasion, particularly the source populations, is an important issue from a pest management perspective. We report a recent invasion of D. suzukii in Ukraine (Yalta, Crimea), with the population having high levels of genetic diversity in contrast to presently characterized populations of D. suzukii from other areas in Europe.

There were apparently two separate invasion routes into Europe and into the USA (Adrion et al. 2014); however, the source(s) of D. suzukii for both regions is unknown. High levels of genetic diversity and sharing of haplotypes between D. suzukii from the USA and SWD samples from China and Japan imply that the invasion of D. suzukii into the USA occurred via a large number of founder individuals and/or from multiple sources of these two areas. We have to note that our haplotype network underestimates the diversity in putative native distribution range of the species, since only four COI sequences from D. suzukii from China could be included in our analysis, as most of the D. suzukii COI sequence data from China had an ambiguous origin (data not shown). In contrast, European SWD was, until now, represented by a predominant haplotype, with a second haplotype found only in Italy; this pattern is consistent with a bottleneck during the foundation of European D. suzukii populations (Adrion et al. 2014). Interestingly, the individuals collected from Yalta (Ukraine) revealed no genetic signature of a sharp bottleneck, and the haplotype sharing with SWD populations from both the USA and Europe suggests that there have been multiple sources of invasion into Ukraine by D. suzukii. It is possible that D. suzukii had been established in Yalta for a significant period of time prior to our sampling and was introduced one or few times but with many individuals that maintained a genetically diverse pool. While it is hard to determine the route and timing of the invasion by D. suzukii into Crimea, the latter scenario seems highly unlikely since all of our sampling localities had been surveyed for Drosophila species annually since 2005 (Kozzeretska et al. 2008; Radionov et al. 2011; Serga et al. 2014, 2015). The relevance of this survey effort points to the arrival of D. suzukii in southern Ukraine close to the summer of 2014. Thus, it seems more likely that D. suzukii was recently introduced to Crimea from distinct sources, such as from the two introduced areas (i.e., the USA and Europe) or, alternatively, from the two ancestral areas (i.e.,
Table 1  Sample locations with GPS coordinates, dates, frequencies and total number of individuals (in parentheses) of 14 Drosophilidae species collected from Ukraine during 2014 and 2015

| Population | Yalta | Odesa | Uman’ | Kharkiv | Piryatin | Kyiv | Chornobyl |
|------------|-------|-------|-------|---------|----------|------|-----------|
| GPS coordinates | 44°30’03.0”N | 46°29’13.9”N | 48°45’45.2”N | 49°59’24.3”N | 50°19’35.4”N | 50°21’09.0”N | 51°16’13.7”N |
|  | 34°10’00.0”E | 30°43’51.5”E | 30°14’38.9”E | 36°13’50.4”E | 32°29’35.6”E | 30°28’57.7”E | 30°13’19.6”E |
| Collection date | 27 Aug 2014 | 24 Jun 2015 | 27 Aug 2015 | 22 Jul 2014 | 27 Aug 2015 | 20 Aug 2015 | 20 Aug 2015 |
|  | 26 Jul 2015 | 20 Aug 2015 | 25 Aug 2015 | 1 Oct 2014 | 26 Sept 2015 | 28 Jul 2014 | 20 Aug 2015 |
|  | 2014 | 2015 | 2015 | 2014 | 2015 | 2015 | 2015 |
|  | D. suzukii | 2.57 (11) | 8.54 (10) | 0.21 (1) | 0.21 (1) | 1.30 (4) | 0.54 (1) |
|  | D. buskii | 7 (30) | 2.56 (3) | 7.45 (34) | 2.1 (10) | 0.31 (1) | 23.02 (99) |
|  | D. cameraria | 4.90 (22) | 18.80 (22) | 1.53 (7) | 0.34 (1) | 0.37 (1) | 4.41 (19) |
|  | D. hydei | 12.84 (37) | 17.52 (41) | 9.34 (27) | 0.37 (1) | 1.94 (8) | 12.63 (23) |
|  | D. immigrans | 0.34 (1) | 0.34 (1) | 0.37 (1) | 1.94 (8) | 5.2 (5) | 4.41 (19) |
|  | D. kuntzei | 2.72 (4) | 0.65 (2) | 2.72 (4) | 1.30 (4) | 0.65 (2) | 23.02 (99) |
|  | D. melanogaster | 85.51 (366) | 70.08 (82) | 90.78 (414) | 97.04 (460) | 86.11 (248) | 98.04 (301) |
|  | D. obscura | 99.62 (265) | 89.58 (86) | 99.62 (265) | 98 (404) | 99.62 (265) | 89.58 (86) |
|  | D. phalerata | 0.34 (1) | 0.34 (1) | 0.34 (1) | 0.34 (1) | 0.34 (1) | 0.34 (1) |
|  | D. plebeia | 4.08 (6) | 0.42 (1) | 4.08 (6) | 0.42 (1) | 5.2 (5) | 0.23 (1) |
|  | D. testacea | 0.42 (2) | 0.42 (2) | 0.42 (2) | 0.42 (2) | 0.42 (2) | 0.42 (2) |
|  | D. simulans | 1.04 (3) | 1.04 (3) | 1.04 (3) | 1.04 (3) | 1.04 (3) | 1.04 (3) |
|  | D. transversa | 2.04 (3) | 2.04 (3) | 2.04 (3) | 2.04 (3) | 2.04 (3) | 2.04 (3) |
|  | D. subobscura | 0.21 (1) | 17 (25) | 0.21 (1) | 17 (25) | 1.09 (2) | 1.09 (2) |
| n | 428 | 117 | 456 | 288 | 234 | 289 | 266 | 412 | 322 | 96 | 147 | 307 | 182 | 430 |
China and Japan). However, the allele sharing with other introduced populations makes this latter hypothesis of an independent introduction from the ancestral populations less likely given the high diversity in detected haplotypes. Although *D. suzukii* individuals were collected in Yalta in 2014 and 2015, we do not have molecular analysis data for the SWD individuals from the first year of sampling. However, even potential 2014 SWD samples would not change the overall pattern of genetic diversity of the *D. suzukii* population in Yalta in 2015, although we cannot assess whether there were two different invasions from distinct sources on the two successive years or a unique introduction from an already admixed locality. The finding in Serbia of a different haplotype shared also with USA suggests that other populations in Europe might present an admixed origin with flies from USA, highlighting the need for further population genetic surveys in a more global and temporal scale.

A combination of geographical profiling analyses and data on the trade of fresh fruit made by Cini et al. (2014) suggested that the most likely arrival location of *D. suzukii* into Europe would be the region surrounding Marseilles (southern France), from where it would have subsequently spread across Europe. The importance of marine routes seems to be supported by the first records of *D. suzukii* in California and in Spain, both occurring close to important sea ports (Rota-Stabelli et al. 2013; Cini et al. 2014), as well as examples of dispersal of the *Drosophila* species that follow commercial fruit trafficking routes (Capy and Gibert 2004; Lachaise and Silvain 2004). Indeed, finding *D. suzukii* from Yalta, which is an important commercial and touristic port located on the coast of the Black Sea, is concordant with the idea that movement of fruit by sea routes presents an important dispersal method by *D. suzukii*. Certainly, the port in Yalta annually hosts hundreds of both cruise liners and cargo trade ships from all over the world; however, it remains to be unknown which one contributed the most into *D. suzukii* invasion to Ukraine. Unfortunately, the combination of (1) reports of *D. suzukii* from other European countries (Asplen et al. 2015) that lack a concomitant molecular analysis [e.g., there are no COI data for *D. suzukii* individuals found in France (Calabria et al. 2012; Withers and Allemand 2012)], (2) published studies that identified multiple individuals with the same haplotype but only reported one sequence (i.e., Calabria et al. 2012; Toševski et al. 2014), underestimating the number of data available from different areas directly obtained from GenBank, and (3) often ambiguous...
Invasion of D. suzukii into Ukraine presents great concern given the enormous economic losses that this species has caused in USA (Wiman et al. 2016) and to some extent in Europe (Asplen et al. 2015). Recent invasions of D. suzukii into some Eastern European countries (e.g., Hungary, Czech Republic, Slovakia, Bulgaria and Serbia) have shown a rapid population expansion after invasion by apparently quite few individuals (Asplen et al. 2015). For example, since D. suzukii was first reported in Serbia in 2014, it rapidly dominated the drosophilid assemblages across the country (Toševski et al. 2014). All individuals of D. suzukii sampled across Serbia shared the same COI haplotype (Toševski et al. 2014), which was identical to the haplotypes from Spain, Portugal, Italy and Japan. However, an additional individual collected from southern Serbia in November of 2014 (that was sequenced after the first report of D. suzukii from Serbia, GenBank accession number: KX273434) (Toševski et al. 2014) shares its COI haplotype with D. suzukii from the USA and China. This again indicates the potential for multiple sources of D. suzukii invasion into Europe, along with possible recurrent introductions of this highly invasive pest species. Thus, in contrast to other analyzed European D. suzukii populations (Adrion et al. 2014, and the present work), D. suzukii from Ukraine and Serbia contain comparatively high levels of genetic diversity that potentially offers a new source of genetic variation in Europe. Establishment of an invasive species often benefits from standing genetic variation that allows greater adaptive potential to new selection pressures (Frankham 2005; Markert et al. 2010; Bouzat 2010). Potentially, rising genetic diversity in D. suzukii populations in Europe, through multiple introductions, can facilitate this species range expansion and increase fruit yield losses caused by this invasive insect pest, possibly also even lessening the impact of biological control agents and pest management activities.

Drosophila suzukii populations dynamics mostly depend on temperature, humidity (Tochen et al. 2014, 2016b; Hamby et al. 2016) and the availability of essential food resources (Tochen et al. 2016a). The dry Mediterranean climate, which is similar to that in Yalta, seems not to be preferred by D. suzukii (Hauser et al. 2009; Calabria et al. 2012). The apparent absence of D. suzukii from continental part of Ukraine therefore may be temporary as these areas apparently have environmental conditions (i.e., temperate climate, milder summer temperatures and higher humidity) that increase fecundity and longevity in D. suzukii (Tochen et al. 2016b). Therefore, the invasion of this pest species into more temperate regions of Ukraine and possible recurrent introductions to other parts of Europe pose a potential threat to agriculture, especially berry crop producers. Currently, it is hard to determine whether the high level of genetic diversity in D. suzukii populations in Yalta is unique, or whether it is a common pattern in other areas across Europe. Further research applying wide range of multilocus genetic markers and more samples from native or invaded D. suzukii areas is needed to provide more resolution. Future studies can make use of the available next-generation sequencing data (Chiu et al. 2013), mitochondrial genes, as well as microsatellites markers (Fraimout et al. 2015), which have been shown to be a powerful tool to understand invasion routes and genetic diversity in Drosophila natural populations (Pascual et al. 2007; Bahder et al. 2015). Results presented herein contribute to identification of D. suzukii global invasion routes and might help to establish this species as a good model object for research on invasion biology and pest management.

Author contributions

IK, SS and AL designed the experiments. AL, IK and SS performed the samplings. AL, IK, MP and FM identified the specimens. AL and JK analyzed data and wrote the manuscript with contribution from all authors. PW supported and assisted the study. All authors read and approved the final version of the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals in research were followed.

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