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Short Communication

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A small survey of introduced *Zaprionus indianus* (Diptera: Drosophilidae) in orchards of the eastern United States

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The African fig fly, *Zaprionus indianus* (Gupta), is a generalist fruit fly that typically breeds in decaying fruits from over 70 plant species. The species has spread globally from its native range in tropical Africa, becoming an invasive pest on ripening figs in Brazil. First reported in the United States in 2005 in Florida, *Z. indianus* has since been documented as far north as Canada and is hypothesized to recolonize northwards from southern refugia each year. We sampled drosophilid communities over the growing season at 2 orchards in Virginia from 2020 to 2022 and 11 orchards along the East Coast during the fall of 2022 to quantify the abundance of *Z. indianus* relative to other drosophilids across locations, seasons, and fruit crops. Massachusetts had the northernmost population, with no *Z. indianus* detected in Maine and no correlation between latitude and relative abundance. Variation in *Z. indianus* relative abundance was high between nearby orchards and abundance was higher on peaches relative to apples within orchards. Comparisons of seasonal abundance curves between 2 Virginia orchards showed similar dynamics across years with individuals first detected around July and becoming absent around December, with peaks in late summer and mid-fall. The variation in seasonal and latitudinal abundance shown here highlights a need for broader sampling to accurately characterize the range, spread, and environmental tolerances of *Z. indianus* in North America.

Keywords: Drosophilidae, ecology and population dynamics, cold hardiness, egg production, fruit tree entomology

Introduction

The African fig fly, *Zaprionus indianus* (Gupta), is an invasive drosophilid originating from tropical Africa (Yassin et al. 2008) that has spread to the Americas, Europe, and the Middle East in recent decades (Al-Jboory and Katbeh-Bader 2012, Kremmer et al. 2017, Molina-Rodríguez and Pérez-Guerrero 2019). Notably, *Z. indianus* was identified in Brazil in 1999 (Vilela 1999) where it is a pest of commercial fig crops (Oliveira et al. 2013). *Zaprionus indianus* was first found in the United States in 2005 in Florida (Van der Linde et al. 2006) and subsequently Virginia in 2012 (Pfeiffer et al. 2019). Populations in North America have been reported as far north as Minnesota, USA (Holle et al. 2019) and Quebec, Canada (Renkema et al. 2013). *Zaprionus indianus* likely does not survive year round in temperate locales but rather recolonizes northward each year from southern refugia (reviewed in Pfeiffer et al. 2019), though Joshi et al. (2014) speculated it overwintered in Pennsylvania.

Zaprionus indianus is a generalist that breeds mainly in fallen or damaged fruit, with the notable exception of figs (Pfeiffer et al. 2019). In Africa, *Z. indianus* has been reported to use more than 70 host species in over 30 families (Lachaise and Tsacas 1983, Yassin and David 2010) plus additional species where it has been introduced (Leão and Tidon 2004, Van der Linde et al. 2006). In many hosts, *Z. indianus* are found in high numbers compared to other drosophilids (Silva et al. 2005, Roque et al. 2017, Pfeiffer et al. 2019). Although *Z. indianus* is primarily a secondary pest that relies on damaged fruits, the possibility exists of unaided infestation in ripened peaches, strawberries, nectarines, plums, and grapes (Joshi et al. 2014, Bernardi et al. 2017, Pfeiffer et al. 2019).

Describing when and where introduced species are found is essential to understanding their impact and informing management solutions, but the seasonal dynamics and variation in abundance of *Z. indianus* are not known. The purpose of this study was to document *Z. indianus* relative abundance in select orchards in the eastern United States to facilitate future work on the ecology, evolution, and genetics of this species. We sampled drosophilid communities at 2 orchards in Virginia from 2020 to 2022 and 11 orchards along the East Coast during the fall of 2022 to quantify the relative abundance of *Z. indianus* across locations, seasons, and fruit crops. Given the Afrotropical origin of *Z. indianus* and the possibility that flies recolonize northerly sites each year, we hypothesized that the abundance of *Z. indianus* at northern latitudes is relatively low and its seasonal dynamics are consistent with local extirpation and reintroduction in Virginia.

Materials and Methods

Field Sampling

To assess the seasonal dynamics of *Z. indianus* populations, collections were conducted every 2–4 weeks in June through December from 2020 to 2022 (excluding June 2020 and December 2021) at 2 orchards in Virginia (Charlottesville and Richmond, 116 km apart). Peaches (*Prunus persica*) are harvested in the summer and apples (*Malus domestica*) are harvested in the fall at both orchards. Latitudinal sampling was conducted in 2022 between 30 September and 14 October from 11 sites spanning 18.5° latitude. All sites were "pick-your-own" orchards, except in Florida, where we sampled in a park growing a variety of tropical fruits distributed in patches (but neither apples nor peaches were available).

Sampling was conducted by netting above fallen fruit with 25.4-cm-diameter nets with 240-μm mesh (Bioquip, Rancho Dominguez, CA) and unbiased aspiration of flies directly from fallen fruit. The choice of method was necessitated by temperature, precipitation, and fly activity. Additionally, traps made from 2-Liter plastic bottles with a 10-cm horizontal slit cut in one side and baited with sliced bananas (*Musa acuminata*) and baker's yeast (*Saccharomyces cerevisiae*) were hung from trees in Charlottesville in 2021 and 2022. Flies aspirated from the traps were combined with netted flies for counting. Flies were sorted under a stereomicroscope to determine counts of *Z. indianus* and other drosophilids. All reported relative abundances reflect the proportion *Z. indianus* in the population and therefore account for differences in overall fly abundance due to resource availability or other environmental factors.

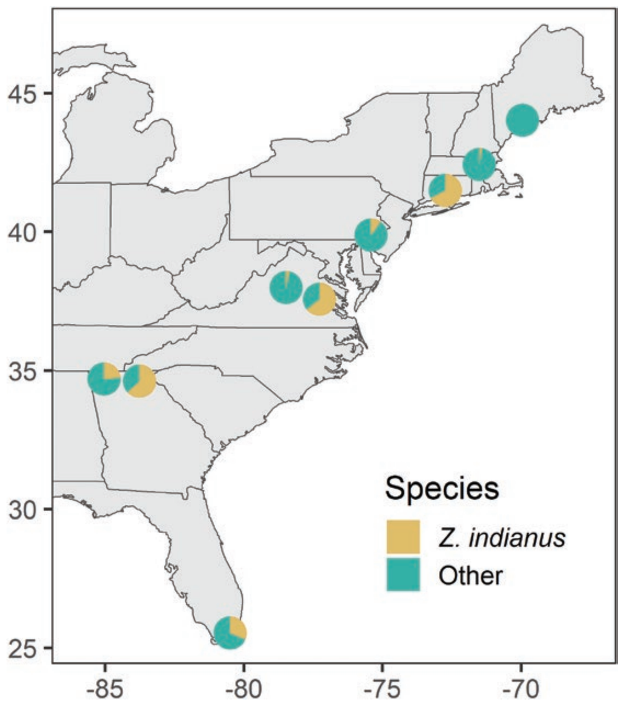

Fig. 1. Abundance of *Zaprionus indianus* relative to other drosophilid species at selected sites sampled on the east coast of the United States in early fall 2022. All individuals were collected on or near apples except in Florida (various fruits). See Table 1 for additional information. The longitudes of Georgia pie charts were adjusted for visibility.

Statistical Analyses

Because our collections came from multiple sampling methodologies, we tested for an effect of netting versus aspirating on *Z. indianus* relative abundance using 14 time points when both methods were used. We used a mixed-effects logistic regression (McCullagh and Nelder 1989) implemented with *glmmTMB* (Brooks et al. 2017) in R (R Core Team 2023, v.4.2.3). *Species* of individual flies (n = 4,566) was coded as the binary response (*Z. indianus* = 1, other species = 0) with *sampling method* and *fruit* (apples vs. peaches) as explanatory variables and *date* as a random effect. Sampling methodology had a marginal (P = 0.05) effect, with the odds of sampling *Z. indianus* from netting 17% higher than from aspirating (Supplementary Table S1). Given the marginal effect, we combined data from netting and aspirating to facilitate further analyses with sufficient sample sizes.

A Pearson's correlation was used to test the association between latitude and proportion of *Z. indianus* relative to other drosophilids (n = 10 orchards; Charlottesville was excluded because trapping was used in addition to netting). We restricted the analysis to flies captured near apples for all sites except Florida (all fruits).

To assess how *Z. indianus* relative abundance varied near different fruits sampled on the same day (7 time points), we used logistic regression with *species* as a binary response (n = 3,641). The *fruit* above which flies were collected (peaches vs. apples) was included as a factor and *Julian date* was included to account for repeated sampling. For the comparison of 8 fruits in Florida (n = 2,187), *fruit* was the only predictor. We used the *drop1* function in R to perform an analysis of deviance to test the significance of multi-level predictors on relative abundance (Zuur et al. 2009).

We used a similar model to analyze the Virginia seasonal sampling. *Species* was the binary response variable (n = 14,643) with *year* (2020–2022), *month* (June-December), and *location* (Richmond, Charlottesville) as predictors assessed with *drop1*. Data including trapped flies were excluded, but the models produced similar results with these years included. Data were managed with

Table 1. Geographic variation in *Zaprionus indianus* abundance relative to other drosophilids in 2022

City	State	Latitude	Longitude	Fruit	Sampling method	Relative abundance	Total collected	Collection date
Bowdoin	ME	44.025	−69.943	Apples	Net	0.00	20	8 Oct
Yarmouth	ME	43.834	−70.239	Apples	Net	0.00	13	8 Oct
Stow	MA	42.430	−71.504	Apples	Net/Aspirator	0.03	153	12 Oct
Stow	MA	42.411	−71.514	Apples	Net	0.02	377	12 Oct
Middlefield	CT	41.494	−72.730	Apples	Net/Aspirator	0.67	446	13 Oct
Media	PA	39.885	−75.410	Apples	Aspirator	0.10	208	14 Oct
Charlottesville	VA	37.991	−78.472	Apples	Trap/Net	0.03	102	4 Oct
Richmond	VA	37.572	−77.266	Apples	Net/Aspirator	0.64	176	6 Oct
Ellijay	GA	34.700	−84.534	Apples	Net	0.23	699	30 Sep
Ellijay	GA	34.620	−84.373	Apples	Net	0.63	438	30 Sep
Homestead	FL	25.535	−80.493	Multiple	Net	0.31	2187	2 Oct

Table 2. Variation in *Zaprionus indianus* relative abundance between apples and peaches. Flies were collected near fruits by netting and aspirating. The total number of drosophilids collected is shown in parentheses

Location	Collection Date	Apples	Peaches
Charlottesville	21 Aug 2020	0.19 (81)	0.49 (300)
Charlottesville	4 Sept 2020	0.39 (76)	0.33 (662)
Charlottesville	18 Sept 2020	0.18 (268)	0.31 (416)
Charlottesville	30 Sept 2020	0.18 (282)	0.29 (92)
Richmond	17 Aug 2022	0.83 (6)	0.68 (433)
Massachusetts	12 Oct 2022	0.03 (153)	0.11 (37)
Pennsylvania	14 Oct 2022	0.10 (208)	0.54 (627)
Total		0.16 (1074)	0.45 (2567)

Table 3. Logistic regression of *Zaprionus indianus* relative abundance on peaches versus apples. Estimates and standard errors are reported as log odds. Residual deviance: 4,466.2 on 3,638 degrees of freedom.

Parameter	Estimate	SE	Z	*P*-value
Intercept	0.562	0.477	1.177	0.239
Peaches	1.330	0.094	14.091	<0.001
Date	−0.008	0.002	−4.663	<0.001

Table 4. Variation in *Zaprionus indianus* relative abundance across various fruit at a single park in Florida. All flies were collected by netting above fallen fruits

Fruit	Relative abundance	Total collected
Marula (*Sclerocarya birrea*)	0.54	218
Sun sapote (*Licania platypus*)	0.48	102
Hog plum (*Spondias mombin*)	0.47	494
Papaya (*Carica papaya*)	0.37	203
Starfruit (*Averrhoa carambola*)	0.29	675
Breadfruit (*Artocarpus altilis*)	0.05	76
Bael (*Aegle marmelos*)	0.03	40
Avocado (*Persea americana*)	0.02	379

data.table (Dowle and Srinivasan 2021) and plotted with *ggplot2* (Wickham 2016).

Results

Latitudinal Survey

We collected 5,561 drosophilids (34.4% *Z. indianus*) in fall 2022. No *Z. indianus* were captured in Maine, and *Z. indianus* made up only 2-3% of drosophilids at the 2 Massachusetts orchards. The relative abundance of *Z. indianus* varied widely across sites (Fig. 1, Table 1) and did not correlate with latitude (t = −1.26, df = 8, P = 0.243, r = −0.41).

Fruit Associations

Within orchards, *Z. indianus* relative abundances were significantly higher near peaches on days when both peaches and apples were sampled (Tables 2 and 3). In Florida, *Z. indianus* relative abundance differed significantly among fruits (analysis of deviance: χ^2 = 391.06, df = 7, P < 0.001, residual deviance: 2,326.5 on 2,179 df). *Zaprionus indianus* was most abundant near marula and least abundant near breadfruit, bael, and avocado (Table 4).

Seasonal Abundance

From 2020 to 2022, we collected 22,650 drosophilids (29.5% *Z. indianus*) from the Richmond and Charlottesville orchards. In both locations, *Z. indianus* showed similar population dynamics across years (Fig. 2). The first *Z. indianus* were generally captured from mid-July to early August, except for one individual captured in June 2022 (Table 5). The populations reached peak abundance in late summer. For most years, a second peak occurred in October, and numbers were low or undetectable by December (Fig. 2, Table 5). The odds of collecting *Z. indianus* in Richmond were 6 times higher than in Charlottesville (Supplementary Table S2), and *Z. indianus* populations in Richmond reached higher relative abundance, peaking at ~80–90% compared to a maximum of ~40–45% in Charlottesville (Fig. 2). Year and month were significant predictors of *Z. indianus* relative abundance (Table 6), indicating substantial temporal variation in populations.

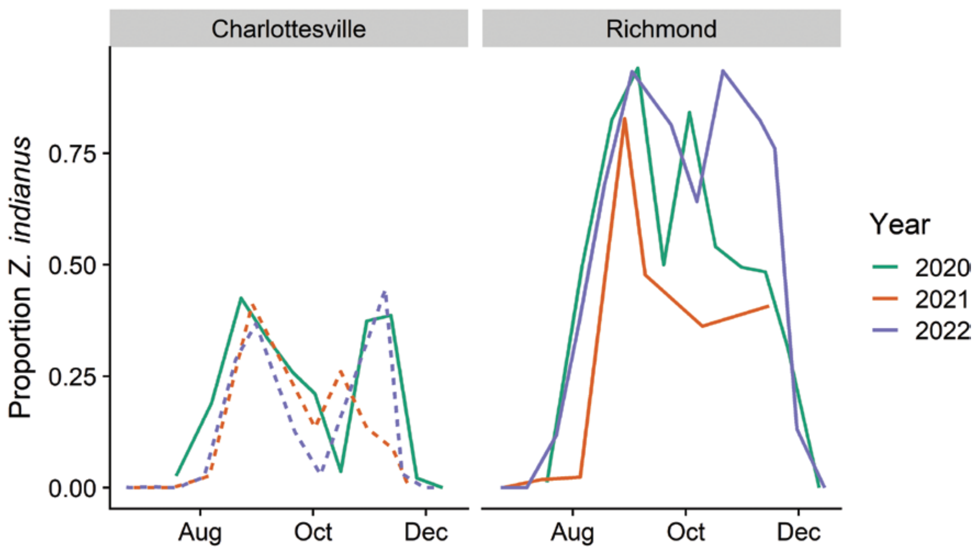

Fig. 2. Seasonal abundance of *Zaprionus indianus* collected from 2 locations in Virginia as a proportion of all drosophilids sampled. Flies were collected near peaches and apples. Solid lines indicate collections done by netting and aspirating. Dashed lines indicate netting and trapping.

Table 5. Dates and relative abundance of first and last capture of *Z. indianus* by location (C = Charlottesville, VA; R = Richmond, VA) and year

Year	Location	Total drosophilid captures	Date of first *Z. indianus* capture	Relative abundance first capture (total drosophilids)	Total drosophilids sampled prior to first capture	Date of last *Z. indianus* capture	Relative abundance last capture (total drosophilids)	Total drosophilids sampled after last capture
2020	C	6,109	17 Jul	0.03 (852)	NA[a]	24 Nov	0.02 (1087)	132
2020	R	4,213	16 Jul	0.01 (414)	NA[a]	23 Nov	0.32 (273)	291
2021	C	2,430	5 Aug	0.03 (483)	99	20 Nov	0.01 (331)	NA[b]
2021	R	2,642	14 Jul	0.02 (108)	137	14 Nov	0.41 (130)	NA[b]
2022	C	5,570	21 Jun	0.001 (751)	0	17 Nov	0.03 (32)	53
2022	R	1,686	22 Jul	0.12 (34)	15	29 Nov	0.13 (99)	28

[a]*Z. indianus* were caught during first sampling in 2020.
[b]Last sampling date of 2021.

Table 6. Predictors in logistic regression analysis of *Zaprionus indianus* seasonal relative abundance assessed by analysis of deviance. Approximate *P*-values computed from Chi-square distribution with *drop1* analysis. Residual deviance: 15,265 on 14,633 degrees of freedom. Full regression output available in Supplementary Table S2

Term dropped	df	Deviance	Difference	*P*-value
None		15,265		
Location	1	16,675	1,410.16	<0.001
Year	2	15,715	450.15	<0.001
Month	6	17,393	2,128.06	<0.001

Discussion

We describe variation in *Z. indianus* relative abundance across locations, seasons, and fruits in select orchards in the eastern United States. Our estimates of *Z. indianus* abundance are limited by small sample sizes, uneven sampling efforts across sites, the use of multiple collection methods, and a lack of sampling in the species' full reported range, but provide insight into its spread, fruit usage, and seasonal dynamics in temperate habitats.

Here, we report the first documentation of *Z. indianus* in Massachusetts, our northernmost capture in 2022. We detected no *Z. indianus* in Maine, but total captures were low and *Z. indianus* could have existed at undetectable levels. Indeed, previous sampling by Renkema et al. (2013) found *Z. indianus* at similar latitudes to our Maine collections, showing that *Z. indianus* reaches those latitudes, although seemingly inconsistently. Similarly, detections one year but not the next have been reported in Kansas (Gleason et al. 2019) and Minnesota (Holle et al. 2019), which may indicate these locations are at the edge of its range. Below an apparent threshold at Massachusetts/Maine, *Z. indianus* relative abundance did not vary predictably with latitude but did vary between orchards at similar latitudes. Differences in microhabitat and orchard management may influence the fly community composition. Landscape cover, for example, is correlated to *Drosophila suzukii* abundance (Haro-Barchin et al. 2018). Alternatively, differential usage of specific fruit cultivars by *Z. indianus* may influence interorchard variation. Additionally, the northern collection locales were more advanced in seasonal phenology at the time of collection, so we cannot deconvolute the effects of latitude and season.

We also found that *Z. indianus* were more common near peaches compared to apples and abundance varied widely on other fruits in Florida. Soft, thin-skinned fruits near ripeness seem to be most at risk of infestation by *Z. indianus* (Steck 2005, Bernardi et al. 2017). "Pick-your-own" orchards where peaches are tree-ripened could be potential targets of *Z. indianus* (Joshi et al. 2014), but further testing is required to confirm this possibility. Prior attack by *D. suzukii* facilitates *Z. indianus* infestation and could also contribute to variation in relative abundance across fruits and orchards (Bernardi et al. 2017, Pfeiffer et al. 2019, Souza et al. 2020). The variable abundance of *Z. indianus* on a range of hosts (Fanara et al. 2022, Ribeiro et al. 2023) underscores the need to identify susceptible targets of attack.

Across three years of sampling, typical first captures of *Z. indianus* in Virginia occurred in July or August despite detection of other drosophilids at earlier dates. A similar trend was seen in Minnesota where *Z. indianus* was first captured even later in September and October (Holle et al. 2019). We did not sample earlier-ripening crops such as berries, so *Z. indianus* may be present in Virginia earlier in the year, a possibility that requires further exploration given its pest potential. In Virginia, *Z. indianus* were usually undetectable by late fall even when other drosophilids were still captured. Late arrival and early decline might indicate yearly local extirpation and recolonization and differ from the seasonal dynamics of the invasive *D. suzukii*, which can persist into January and is thought to overwinter (Thistlewood et al. 2018). Alternatively, *Z. indianus* may take longer to reach detectable population numbers than other drosophilids and/or enter an overwintering state sooner. The possibility of different life-history strategies or environmental tolerances relative to local drosophilids highlights a need for additional comparative studies. The drop in abundance in mid-fall was notable; during the period when most peaches have rotted but few apples are available, *Z. indianus* may lack suitable habitat and drop in abundance, though numerous other biotic or abiotic factors could be at play.

Despite limited samples and localities, our results indicate differences in *Z. indianus* relative abundance between nearby orchards and within individual orchards. We further demonstrate relatively large changes in abundance over short temporal scales (weeks). These findings suggest that numerous environmental factors likely influence the establishment and success of this species. Our findings also highlight a need for systematic sampling to accurately characterize the range and spread of *Z. indianus* over time.

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Author Contributions

Logan M. Rakes (Conceptualization [Equal], Data curation [Lead], Formal analysis [Lead], Investigation [Lead], Visualization [Lead], Writing – original draft [Lead], Writing – review & editing [Lead]), Megan Delamont (Data curation [Equal], Investigation [Equal]), Christine Cole (Investigation [Equal]), Jillian A. Yates (Investigation [Equal]), Lynsey Blevins (Investigation [Equal]), Fatima Hassan (Investigation [Equal]), Alan O. Bergland (Conceptualization [Equal], Funding acquisition [Equal], Project administration [Equal], Supervision [Equal], Writing – review & editing [Equal]), and Priscilla Erickson (Conceptualization [Equal], Data curation [Equal], Formal analysis [Equal], Funding acquisition [Equal], Investigation [Equal], Methodology [Equal], Project administration [Equal], Supervision [Equal], Visualization [Equal], Writing – original draft [Equal], Writing – review & editing [Equal])

Data Availability

All raw data and code are available on Dryad: doi:10.5061/dryad.zw3r228cj.

Supplementary Material

Supplementary material is available at *Journal of Insect Science* online.

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