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Fruit parasitism and abundance of a non-native insect pest affects abundances of some songbirds

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Abstract Non-native insect pests can have significant effects on forest ecosystems. Forest fruit-targeting non-native insect pests may cause extensive damage to fruits, reducing food for fruit-tracking wildlife. Parasitism of forest fruits by spotted wing Drosophila (*Drosophila suzukii*, SWD) may put it in competition for fruits with fruit-consuming forest songbirds during their post-breeding and migration seasons. Our objective was to identify factors, primarily SWD abundance and fruit parasitism, influencing frugivorous and non-frugivorous bird relative abundance and species richness in regenerating timber harvests invaded by SWD in western Pennsylvania during the post-breeding season and fall migration in 2019 and 2020. Eastern towhee (*Pipilo erythrophthalmus*) relative abundance correlated negatively with SWD counts, while hooded warbler (*Setophaga citrina*) relative abundance correlated negatively with fruit parasitism. Most bird relative abundances correlated to vegetation structure or date, not SWD variables. Eastern towhee possibly viewed fly-covered fruits as less desirable for consumption or were deterred by SWD swarms disturbed while foraging on or near the ground. Based on modeling results of hooded warbler, SWD activity may have shifted arthropod community composition and impacted some arthropod-consuming birds via trophic cascading effects: parasitism-induced fruit drop driving arthropod prey from foliage, deterring some foliage-gleaning birds (hooded warbler). Frugivorous birds either did not alter fruit consumption or masked relationships to SWD likely by altering diet and foraging behavior, demonstrating an apparent resilience to invasion complemented by the importance of date. Investigating arthropod communities and consumption of fruits in habitats invaded by SWD are critical next steps to understanding ecological effects of SWD.

Keywords *Drosophila suzukii* · Frugivorous birds · Fruit parasitism · Migration · Post-breeding · Spotted wing *Drosophila*

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Introduction

Globally invasive species play a critical role in determining the abundances of native species in invaded ecosystems (Roemer et al. 2002; Grosholz et al. 2009). Non-native insect pests (NNIPs) compete with and displace native species for food resources, alter habitat structure and suitability for many native taxa, and disrupt trophic interactions through many mechanisms: feeding on plant material, preying or parasitizing on native species, or pollinating native plants (Kenis et al. 2009). Research on the effects of fruit consumption or parasitism by NNIPs shows extensive damage to crops (Moschos 2006; Maistrello et al. 2017), but NNIPs likely consume native, non-crop fruits in nearby alternative fruiting plants (Bakken et al. 2015; Rodriguez-Saona et al. 2018). Native to east Asia, spotted wing Drosophila (SWD, *Drosophila suzukii*) parasitizes many soft-skinned cultivated fruits in agricultural landscapes (Walsh et al. 2011). Since its accidental introduction to California in 2008, SWD has colonized forested ecosystems in the eastern U.S. and has been documented as parasitizing more than 100 different fruiting plant species, including wild plants (Roche et al. 2021). Female SWD oviposit into ripe and ripening fruits (Mitsui et al. 2006) and larvae consume the fruits, promoting microbial infection and premature drop of fruits from the parent plant (Walsh et al. 2011). While fruit parasitism and microbial infection by native insects reduces consumption by vertebrate consumers (Manzur and Courtney 1984; Sallabanks and Courtney 1992), there remains a critical knowledge gap in understanding how fruit consumption or parasitism by NNIPs such as SWD affects native ecosystems, notably the response of vertebrate frugivores to SWD infestation of fruits.

Loss of fruit resources due to SWD parasitism in forested ecosystems has the potential to be especially harmful for migratory songbirds. Many songbirds are under intense energetic demands after the breeding season (i.e., post-breeding season and fall migration) to build and replenish fat deposits needed for successful migration (Blem 1980; Cyr et al. 2008). Many species, including those that are not usually frugivorous, utilize abundant fruit resources during this time of year (Thompson and Willson 1979; Parrish 1997). Fruit-consuming bird use of early successional habitat (e.g., regenerating timber harvests) is correlated with fruit abundance (Major and Desrochers 2012). However, whether fruit-consuming migratory forest bird abundances will be affected by the infestation of fruiting plants by a frugivorous NNIP in forested ecosystems during post-breeding and migratory seasons remains unknown (Roche et al. 2021).

We investigated whether bird community species abundances are affected by SWD invasion in regenerating timber harvests during the post-breeding season and fall in western Pennsylvania, USA. Specifically, do fruit-consuming (frugivorous) birds decrease in relative abundance with greater SWD and fruit parasitism? Our objectives were to: 1) measure relative abundance and species richness of frugivorous and non-frugivorous birds in regenerating harvests during the post-breeding season and fall migration; and 2) determine what factors in regenerating harvests (i.e., SWD counts, fruit resources, fruit parasitism by SWD, and cover provided by vegetation structure) influence frugivore and non-frugivore relative abundance and species richness. While frugivorous birds are flexible in their diets, consuming plant and animal foods to meet nutritional needs (McKinnon et al. 2017), we hypothesized these birds would be most likely to demonstrate a response to SWD. For objective 2, we hypothesized that relative abundance and species richness of frugivores, but not non-frugivores, in regenerating harvests would be negatively associated with SWD counts and fruit parasitism. While there is no evidence of direct or indirect consumption of SWD by migratory songbirds, native bird species may consume NNIPs as a new food resource. Such possibilities offer an alternative hypothesis that birds who consume SWD increase with greater SWD abundance or fruit parasitism by SWD (Barber et al. 2008). We also hypothesized that frugivores, but not non-frugivores, would be positively associated with fruit variables; both guilds would be positively associated with vegetative cover variables representing more complex structure (Vitz and Rodewald 2007).

Methods

Study area

We conducted this study at the Allegheny National Forest (ANF; 41°40′N, 78°05′W), at Clear Creek State Forest (CCSF; 41°18’ N, 79°00’ W), and

on State Game Lands (SGL) 86 (41°43′31'' N, 079°21′29'' W) in the Allegheny High Plateau of northwestern Pennsylvania. The US Forest Service, Pennsylvania Department of Conservation and Natural Resources, and Pennsylvania Game Commission manage these properties, respectively. Dominant tree species include black cherry (*Prunus serotina*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), and multiple oak species (*Quercus* spp.), notably northern red oak (*Quercus rubra*; US Forest Service 2007). Timber harvests occur on each property, producing regenerating harvests of different ages. Regenerating timber harvests contain seedlings and saplings representative of adjacent forest communities and a variety of fruiting plants, including blackberry (*Rubus* spp.), pokeweed (*Phytolacca americana*), pin cherry (*Prunus pennsylvanica*), *Aralia* spp., *Vaccinium* spp., serviceberry (*Amelanchier* spp.), and American (*Sambucus canadensis*) and red elderberry (*S. racemosa*).

Study design

We conducted all sampling 18 July–25 September, 2019 and 20 July–25 September, 2020. This timing coincides with post-breeding phenology (Jun–Aug: Stoleson 2013), onset of migration (mid-Aug–Nov) of locally occurring bird species (S. H. Stoleson, unpublished data), and the observed emergence of SWD in previous years (Turcotte et al. 2018). We randomly selected 21 sites within 3–8-year-old regenerating timber harvests that were spaced at least 2 km apart (Vitz and Rodewald 2006, 2007; Table S1, Fig. 1). We covered each site with a grid of points placed 100 m apart to minimize chance of recapture between mist nets. From this grid we randomly selected 5 points, removing any points within 25 m of harvest boundaries to avoid edge effects. We used the Vegetation dataset from the Allegheny National Forest Geographic Information System (GIS) Dataset collection (US Forest Service 2019) in ArcGIS Pro v. 2.3.0 (ESRI, Redlands, CA, USA) to identify timber harvests for site selection and for placing sampling points. From 2019 to 2020, we sampled 105 points across 21 sites.

Avian sampling

We used constant-effort, passive mist netting (Dunn and Ralph 2004) to sample the bird communities in each regenerating harvest. Birds are less vocal during the post-breeding season, and regenerating harvests have low visibility for detection purposes due to dense vegetation (Pagen et al. 2000), making point counts ineffective at detection and generating accurate estimates of abundance than during the breeding season. By using ground mist nets, we had a greater probability of capturing rare or secretive species. We placed a single net (12 m long, 2.6 m high, 30-mm mesh) at each of the 5 sampling points per site. Recaptures were low during our study (2.81% of all captures); thus, we considered nets to be independent sample units. We visited sites during both the post-breeding (mid-July to mid-August) and migration (mid-August to late September) period. During each period, we sampled sites 2 days in a row (McDermott and Wood 2010), unless adverse weather required a delay of 1–2 days between sampling, in each of 2 periods during the season (mid-Jul to late Sep). Because net captures decline with each additional netting day (Karr 1981), visits lasted 2 days to increase efficiency of detecting birds.

We opened nets 30 min before sunrise and kept nets open for 5 h (Ralph et al. 2004). We banded all birds captured (except Ruby-throated hummingbird [*Archilochus colubris*]) with a United States Geological Survey (USGS) aluminum band. We grouped all captured birds into foraging guilds (non-frugivorous or frugivorous) using existing life history data (i.e., Birds of the World species account) and evidence of extensive frugivory from past mist-netting at the ANF (e.g., stains on bill or in fecal samples; S. H. Stoleson, unpublished data) (Tables S2 and S3).

Fruit sampling

To determine relative availability of fruit resources at each mist net, we conducted fruit surveys for Allegheny blackberry (*R. allegheniensis*), the dominant fruiting plant at our sites, immediately after the first day of netting (McDermott and Wood 2010). At each net lane, we placed 2 parallel transects on a randomly selected side: one "inner" transect 1 m away and one "outer" transect 25 m away from the net (Fig. 2; modified from Vitz and Rodewald

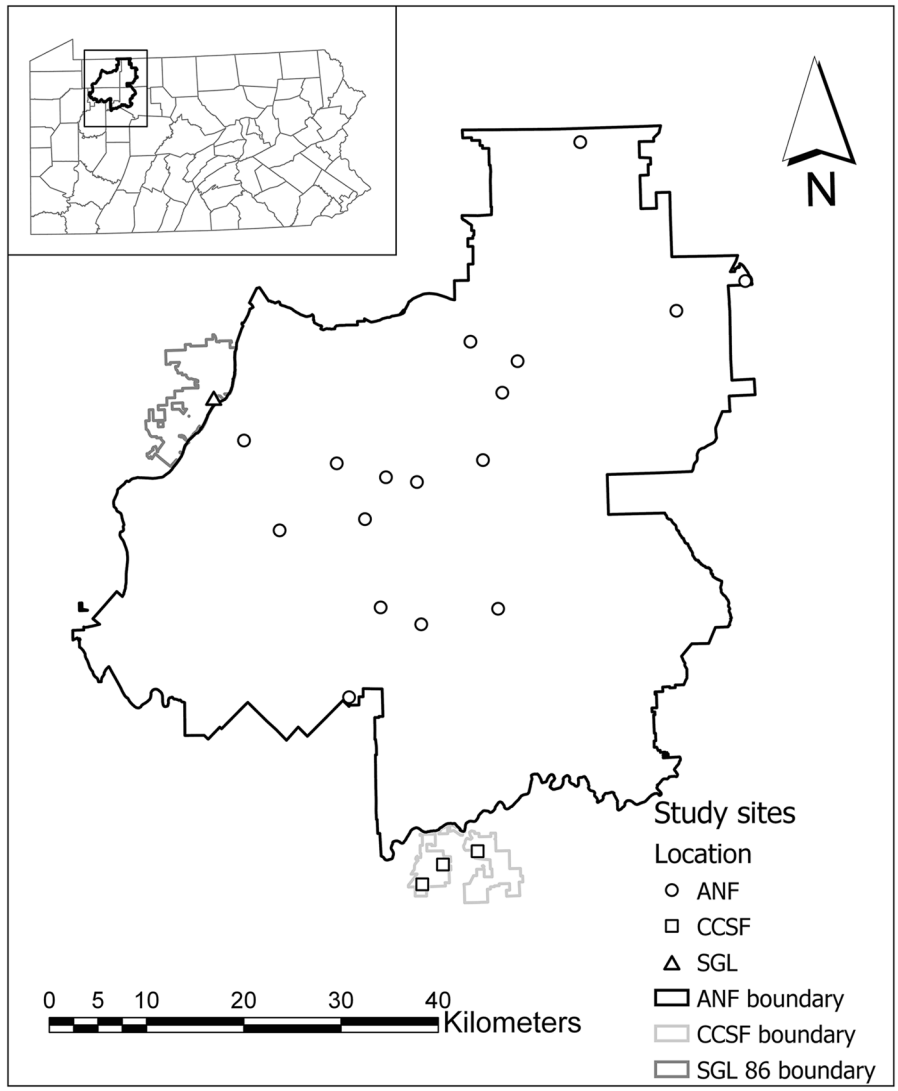

Fig. 1 Study area used for surveys of forest bird communities and spotted wing Drosophila (*Drosophila suzukii*). Twenty-one sites were surveyed across Allegheny National Forest (ANF; 41°40′N, 78°05′W), Clear Creek State Forest (CCSF; 41°18′ N, 79°00′ W) due south, and State Game Lands (SGL) 86 (41°43′31′′ N, 079°21′29′′ W) west of the ANF along the Allegheny River in northwestern Pennsylvania

2006). At 3 m, 6 m, and 9 m along each inner and outer transect, we randomly chose a side and counted the number of unripe (green, still growing) and ripening and ripe (full-size) *R. allegheniensis* fruits within a 0.5-m × 0.5-m quadrat, pooling each quadrat for a single count of unripe fruits and full-size fruits along each transect. Only counting ripe fruits, especially for rapidly ripening plants such as *Rubus* spp., does not reflect the potential availability of fruits to birds (Blake et al. 1990). We also identified all species within each quadrat that produce fleshy fruits, even if not actively fruiting. Finally, we estimated fruiting species richness at each mist net.

Fruit parasitism sampling

We sampled ripening and ripe *R. allegheniensis* fruits along each transect and monitored for emergence of adult, pupal, and larval SWD (20 fruits from each transect, when possible). We weighed fruits within 2 h of collection and stored them, separated by transect, at room temperature (approximately 20 °C) under ambient light in a sealed, vented 473 mL clear container (Webstaurant Store, Lancaster, PA, USA). We checked after a minimum of 2 weeks for adult, larval, and pupal SWD (Walsh et al. 2011). From containers, we pooled total SWD counts and fruit sample masses between transects to determine the infestation

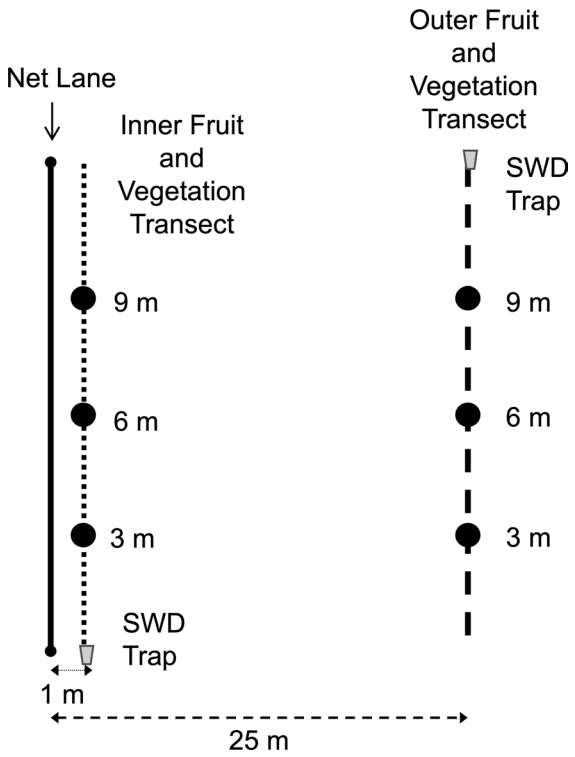

Fig. 2 Transect survey design used to place spotted wing Drosophila (*Drosophila suzukii*, SWD) traps, count fruit resources, and measure vegetation structure at mist nets. The side of the mist net each transect was placed and the side of the transect each SWD trap was placed were randomly chosen

rate of *R. allegheniensis*, measured as the count of SWD per gram of fruit at each mist net (Kenis et al. 2016).

SWD sampling

At the beginning of each site visit, we placed traps to sample for SWD using traps described by Pelton et al. (2016). We placed one trap at the end of each "inner" (1 m) and "outer" (25 m) transect (Fig. 2). We suspended traps approximately 1 m off the ground and close to vegetation to minimize exposure to direct sun and increase likelihood of trap capture (Diepenbrock and Burrack 2017). We collected the contents of each trap following the closing of mist nets at the end of the 2-day site visit and counted all adult SWD in each trap. We pooled counts of SWD from both traps to determine a single count of SWD at each mist net. If a trap fell or was damaged such that the contents were lost, we discarded the trap and saved no sample. To address differences in 1) number of trap samples at each net, and 2) number of days traps were out at a site due to adverse weather delaying banding by 1–2 days, we calculated the count of adult SWD captured per trap per day for each mist net.

Vegetation sampling

To determine vegetation structure at each mist net, we surveyed the vegetation along each "inner" and "outer" transect used for fruit surveys once each year (Fig. 2). At 3 m, 6 m, and 9 m along each transect, we measured vegetation height directly (m) and estimated vertical cover from 2 to 2.5 m above ground using a vegetation profile board (Nudds 1977). The proportion of the board covered by vegetation received a single-digit cover score (1 = 0–20% cover, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%). An observer took measurements at the transect on either side by facing the board perpendicular to the transect from 15 m away. To obtain a single value at each mist net that captured the variation in vegetation height, we calculated the coefficient of variation (CV) using the 6 height values measured along both transects (3 per transect). We also calculated CV values for vertical cover at each mist net using the 12 ordinal values measured (6 per transect). We also measured dbh of any residual trees within 25 m of the center of each mist net lane to calculate a residual tree basal area at each mist net.

Data analysis

From bird capture data, we recorded rates of individual species captures at each mist net during each sampling period. Total number of observations for analyses was 105 mist net locations multiplied by 2 sampling periods ($n = 210$). We only included birds in analyses the first time they were captured during each 2-day sampling period. Birds were rarely captured twice during the same sampling period (40 recaptures out of 2671 total captures). From the list of individual species captured, we chose 6 focal frugivore species and 7 focal non-frugivore species for analyses. For frugivorous birds, our focal species were: cedar waxwing (*Bombycilla cedrorum*), eastern towhee (*Pipilo erythrophthalmus*), gray catbird (*Dumetella carolinensis*), ovenbird (*Seiurus aurocapilla*), red-eyed vireo (*Vireo olivaceus*), and song sparrow

(*Melospiza melodia*; Table 1). We chose these 6 species as our focal frugivorous species because they showed the highest capture numbers and, while life history accounts (i.e., Birds of the World) may suggest different degrees of frugivory among these species, they have shown frequent evidence of fruit consumption at the ANF previously (S. H. Stoleson, unpublished data). For non-frugivorous birds, our focal species were: American redstart (*Setophaga ruticilla*), black-capped chickadee (*Poecile atricapillus*), black-throated green warbler (*Setophaga virens*), chestnut-sided warbler (*Setophaga pensylvanica*), common yellowthroat (*Geothlypis trichas*), hooded warbler (*Setophaga citrina*), and magnolia warbler (*Setophaga magnolia*; Table 1). From captures of all individual species, we derived total captures and species richness at the guild level (frugivore and non-frugivore).

Prior to analysis, we tested for collinearity among predictor variables and eliminated any variables with an absolute value of a correlation coefficient ≥ 0.7 (Dormann et al. 2013). For example, we pooled fruit counts from each quadrat from each transect (1 m and 25 m from the mist net) and SWD trap captures from each transect at each mist net. Fruit counts (as used in analyses) and both SWD variables (trap captures and fruit infestation rate) were not strongly correlated; thus, we considered them sufficiently independent to be included in the same analyses, and any relationships of bird abundances to SWD trap captures or fruit infestation rates would be independent of any relationship to fruit availability. We chose 9 final covariates for analyses (Tables 2 and 3). We included date as an additional covariate to account for the temporal component to sampling and for possible phenological shifts in bird habitat use following the breeding season and during migration.

To model all bird capture variables (i.e., focal species captures, total guild captures, guild species richness), we fit generalized linear mixed models (GLMMs) using a Bayesian approach with Markov-chain Monte-Carlo (MCMC) parameter estimation techniques. Because recapture rates were too low to utilize mark-recapture models (14 recaptures out of 1233 total captures in period 2), we modeled counts of focal species, individuals within each dietary guild, and species richness of each dietary guild at mist net i during sampling period j (all denoted $y_{i,j}$) as Poisson random variables:

$$y_{i,j} \sim \text{Pois}\left(\lambda_{i,j}\right),$$

We assumed expected counts ($\lambda_{i,j}$) were a log-linear function of covariates, a random point (i.e., mist net) effect to account for repeated observations at the same mist net, and a random year effect to account for observations made in 2019 or 2020:

Table 1 Captures and dietary guild identity of focal bird species captured. Sampling periods 1 and 2 correspond approximately to the post-breeding and fall migration periods, respectively

Common name	Scientific name	Family	Guild	Period 1 captures	Period 2 captures
Cedar waxwing	*Bombycilla cedrorum*	Bombycillidae	Frugivore	99	12
Eastern towhee	*Pipilo erythrophthalmus*	Passerellidae	Frugivore	32	26
Gray catbird	*Dumetella carolinensis*	Mimidae	Frugivore	134	80
Ovenbird	*Seiurus aurocapilla*	Parulidae	Frugivore	36	35
Red-eyed vireo	*Vireo olivaceus*	Vireonidae	Frugivore	124	51
Song sparrow	*Melospiza melodia*	Passerellidae	Frugivore	86	19
American redstart	*Setophaga ruticilla*	Parulidae	Non-frugivore	42	19
Black-capped chickadee	*Poecile atricapillus*	Paridae	Non-frugivore	9	60
Black-throated green warbler	*Setophaga virens*	Parulidae	Non-frugivore	22	85
Chestnut-sided warbler	*Setophaga pensylvanica*	Parulidae	Non-frugivore	346	129
Common yellowthroat	*Geothlypis trichas*	Parulidae	Non-frugivore	87	110
Hooded warbler	*Setophaga citrina*	Parulidae	Non-frugivore	35	38
Magnolia warbler	*Setophaga magnolia*	Parulidae	Non-frugivore	34	107

Table 2 Final covariates used to model bird captures at mist nets. Multiple measures were pooled for a single value of each covariate at each mist net and checked for collinearity ($r \geq 0.7$). All covariates were included in a global model for each bird variable, which were then excluded from final models using a stepwise removal process

Covariate category	Covariate name	Description
Date	date	Ordinal date of first bird banding day of each 2-day banding session
Fruit	unripe	Count of unripe Allegheny blackberry (*Rubus allegheniensis*) fruits at each mist net
Fruit	ripen.ripe	Count of ripening and ripe *R. allegheniensis* fruits at each mist net
Fruit	max.richness	Maximum count (over all sampling periods) of plant species at each mist net that produce fleshy fruits
SWD	swd	Count of spotted wing Drosophila (*Drosophila suzukii*, SWD) per trap per 24 h at each mist net
SWD	infest	Count of adult, larval, and pupal SWD per gram of *R. allegheniensis* fruit at each mist net
Veg	BA	Residual tree basal area within 25 m of each mist net (m^2)
Veg	height	Coefficient of variation for vegetation height measurements (m) at each mist net
Veg	cover	Coefficient of variation for cover score values at 2–2.5 m at each mist net

Table 3 Summary of covariate data collected at mist nets. Data are separated into sampling period 1 (18 Jul–22 Aug 2019 and 20 Jul–25 Aug 2020), sampling period 2 (24 Aug–25 Sep 2019 and 27 Aug–25 Sep 2020), and both sampling periods combined. If values at each mist net did not differ from sampling period 1 to 2, values are only reported for period 1

Covariate	Period 1			Period 2			Periods 1 and 2		
	Mean (SE)	Median	Range	Mean (SE)	Median	Range	Mean (SE)	Median	Range
Unripe Allegheny blackberry (*Rubus allegheniensis*) fruits	66.22 (6.88)	45	0–386	0.52 (0.14)	0	0–7	33.37 (4.12)	0.5	0–386
Ripening and ripe *R. allegheniensis* fruits	40.57 (5.05)	26	0–325	2.54 (0.60)	0	0–37	21.56 (2.86)	2.5	0–325
Fruiting species richness	2.53 (0.11)	2	1–5						
Spotted wing Drosophila (SWD) trap captures per trap per day	67.67 (9.97)	23	1–569.5	327.79 (44.47)	153	1.5–2338.5	197.73 (24.45)	61.25	1–2338.5
Infestation rates (SWD per gram of fruit)	4.04 (0.42)	3.03	0–18.89	0.67 (0.16)	0	0–7.05	2.36 (0.25)	0	0–18.89
Residual tree basal area (m^2)	0.40 (0.05)	0.27	0–2.51						
Vegetation height CV[a]	37.35 (1.55)	35.39	11.22–94.11						
Vertical cover CV[a]	39.30 (1.98)	38.38	0–87.09						

[a]denotes a coefficient of variation (CV)

$$\log\left(\lambda_{i,j}\right) = \alpha_i + X\beta + \varepsilon_k,$$

where α_i is the random intercept associated with mist net i, X is the design matrix, β is the vector of slope coefficients, and ε_k is the random error associated with year k. To assess the goodness-of-fit (GOF) of individual models, we calculated a Bayesian p value using the sum of squared Pearson residuals (Gelman et al. 2004). If a model variable failed this GOF test (p value less than 0.1 or greater than 0.90), we treated that response variable as a negative binomial (NB) random variable and re-ran the model using NB regression:

$$y_{i,j} \sim \mathrm{NB}\left(p_{i,j}, r\right),$$

$$p_{i,j} = \frac{r}{r + \lambda_{i,j}},$$

$$\log\left(\lambda_{i,j}\right) = \alpha_i + X\beta + \varepsilon_k,$$

where r is the dispersion parameter, $\lambda_{i,j}$ is the expected count, and we use moment matching to translate expected counts and the dispersion parameter into parameters into the NB success probability parameter $p_{i,j}$ (Hooten and Hobbs 2015).

To determine which covariates to conduct final inference on, we performed stepwise regression on each response variable. First, we ran a global model for each response variable containing all 9 covariates and performed the GOF test to determine which distribution to use (Poisson or NB). Second, we removed all covariates with a marginal posterior estimate for a slope coefficient (β) that had a 90% credible interval (CI) overlapping 0. We ran the reduced model and performed the GOF test, using the same criterion to remove covariates. We repeated this process until all remaining covariates had a 90% CI that did not overlap 0. We conducted covariate removal and final inference using 90% CIs to identify potentially weak but ecologically meaningful effects, given our relatively small sample size. We conducted all stepwise regression for each response variable using the same distribution as the global model (Poisson or NB). All reduced models passed the GOF test regardless of distribution used for the response variable.

We ran all models using software JAGS version 4.3.0 (Plummer 2003) called from R version 4.0.3 (R Core Team 2021) using communicator package jagsUI version 1.5.2 (Kellner 2019). We drew random intercepts (α_i) and random errors (ε_k) from a Normal distribution with mean α and precision τ_α (1/variance):

$$\alpha_i \sim N\left(\alpha, \tau_\alpha\right),$$

$$\varepsilon_k \sim N\left(\alpha, \tau_\alpha\right).$$

We specified Normal priors for the population-level intercept mean (α):

$$\alpha \sim N(0, 0.01),$$

where 0 is the mean and 0.01 is the precision. We derived precision τ_α from a standard deviation with a uniform prior:

$$\tau_\alpha = \frac{1}{\sigma_\alpha^2},$$

$$\sigma_\alpha \sim \mathrm{Unif}(0, 10).$$

We assumed Normal priors for slope coefficients with mean 0 and precision 0.01:

$$\beta_{\mathrm{covs}} \sim N(0, 0.01).$$

For NB models, we used a uniform prior for the dispersion parameter, r, with a large upper bound:

$$r \sim \mathrm{Unif}(0, 50).$$

We ran 3 MCMC chains for each model. We used traceplots to determine an appropriate burn-in for each model, and we ran each model for enough iterations to achieve convergence. We confirmed convergence of models by checking that the Gelman–Rubin diagnostic (Rhat) values for all model parameters were < 1.1 (Gelman et al. 2004). Burn-in lengths and number of iterations necessary for convergence of all models ranged from 10,000 to 35,000 and 20,000 to 70,000, respectively. We thinned iterations by 2 to help reduce autocorrelation between posterior draws.

Results

Bird captures

We captured 2630 birds of 80 species throughout the study for inclusion in guild richness and total abundance modeling. Of these, 951 were from 27 species defined as frugivorous, and 1679 were from 53 species defined as non-frugivorous. Captures were dominated by catbirds (Family: Mimidae, 23%), vireos (Family: Vireonidae, 21%), sparrows (Family: Passerellidae, 17%), and waxwings (Family: Bombycillidae, 12%) for frugivores, and warblers (Family: Parulidae, 86%) for non-frugivores (Tables S2 and S3). Captures of the 13 focal species accounted for most captures under each guild definition (Tables S2 and S3). Several of the 13 focal species chosen for modeling showed large differences in captures from sampling period 1 to 2 (Table 1).

Model results

Final models for all guild-level variables (total abundance and species richness) did not include SWD trap capture or SWD infestation rate (Table 4). Final models for 5 of 6 focal frugivore species and all non-frugivore species lacked SWD trap captures, while all final models for frugivore species and 6 of 7 non-frugivore species lacked SWD infestation rate (Table 4). Only eastern towhee and hooded warbler relative abundances were negatively correlated to SWD trap captures and infestation rates, respectively (Table 4).

Remaining frugivore species relative abundance was correlated to different combinations of date, fruit, and vegetation variables, which differed for relative guild abundance, guild richness, and among species (Table 4). As a guild, frugivore and 3 focal species relative abundances (cedar waxwing, red-eyed vireo, song sparrow) exhibited greatest relative abundances early in the season. Gray catbird relative abundance

Table 4 Final regression models for bird captures by species and guild. Each final model was created with a stepwise removal process of covariates from a global model containing all 9 covariates. Posterior estimates and 90% credible intervals (CIs) are given for each covariate's slope coefficient

Response variable	Distribution	Covariate (Estimate [90% CI])
Frugivore guild level		
Total frugivores	Negative binomial	date (−0.277 [−0.372, −0.181])
Frugivore species richness	Poisson	none
Frugivore species		
Cedar waxwing	Poisson	date (−1.085 [−1.334, −0.847])
Eastern towhee	Poisson	swd (−0.317 [−0.647, −0.028]); cover (0.383 [0.138, 0.616])
Gray catbird	Poisson	max.richness (0.263 [0.088, 0.441])
Ovenbird	Poisson	max.richness (−0.392 [−0.672, −0.123])
Red-eyed vireo	Negative binomial	date (−0.435 [−0.646, −0.225]); cover (−0.306 [−0.548, −0.062])
Song sparrow	Poisson	date (−0.805 [−1.005, −0.610]); BA (−0.471 [−0.747, −0.210]); cover (0.350 [0.155, 0.553])
Non-frugivore guild level		
Total non-frugivores	Negative binomial	unripe (0.109 [0.025, 0.192]); ripen. ripe (−0.127 [−0.220, −0.035])
Non-frugivore species richness	Poisson	date (0.098 [0.042, 0.155])
Non-frugivore species		
American redstart	Poisson	date (−0.432 [−0.666, −0.195]); cover (−0.391 [−0.730, −0.072])
Black-capped chickadee	Poisson	date (1.359 [0.917, 1.856]); unripe (0.514 [0.035, 0.991]); height (−0.506 [−0.992, −0.048])
Black-throated green warbler	Poisson	date (0.809 [0.602, 1.028])
Chestnut-sided warbler	Negative binomial	date (−0.638 [−0.764, −0.516])
Common yellowthroat	Poisson	cover (0.376 [0.210, 0.545])
Hooded warbler	Poisson	infest (−0.376 [−0.682, −0.105])
Magnolia warbler	Poisson	date (0.677 [0.509, 0.851]); cover (−0.274 [−0.488, −0.056])

was positively correlated to fruiting species richness, while ovenbird was negatively correlated. Three focal species (eastern towhee, red-eyed vireo, and song sparrow) relative abundances were correlated to vegetation variables (Table 4). No other relationships to date, fruit, or vegetation variables were apparent.

Non-frugivores also showed varying relationships to date, fruit, and vegetation variables. Species richness and 3 focal species (black-capped chickadee, black-throated green warbler, and magnolia warbler) exhibited greatest relative abundances late in the season, while 2 species (American redstart and chestnut-sided warbler) exhibited greatest relative abundance early in the season. Total non-frugivore captures were correlated to fruit counts, as was one focal species (black-capped chickadee). Four species (American redstart, black-capped chickadee, common yellowthroat, and magnolia warbler) responded to vegetation variables (Table 4). No other relationships to date, fruit, or vegetation variables were apparent.

Discussion

Of our guilds and 14 individual species abundances, 2 species showed strong, correlative relationships to SWD and not uniformly in the ways we predicted. Relative abundance of eastern towhee, a frugivore, correlated negatively to SWD trap captures but not parasitism of *R. allegheniensis* fruits. Hooded warbler, a non-frugivore, correlated negatively with infestation rates of *R. allegheniensis* fruits but not SWD trap captures, despite a diet primarily comprised of invertebrates (Chiver et al. 2020). These relationships are of heightened importance, as both species are listed in Pennsylvania's 2015–2025 State Wildlife Action Plan (SWAP; PGC-PFBS 2015). We did not investigate the ecological mechanisms by which these species correlated to SWD, but these relationships persisted throughout our models.

Different mechanisms may be at work on eastern towhee and hooded warbler. Adult SWD visibly swarmed in dense undergrowth of plants where birds foraged for fruits, (D. P. Roche, personal observation), a previously nonexistent phenomenon at the ANF (S. H. Stoleson, personal observation). Parasitism by SWD increases fruit drop from the parent plant (Walsh et al. 2011) and SWD will exploit fruit on the ground (Bal et al. 2017). As a ground forager, eastern towhee would have disrupted SWD while leaf-tossing in search of food (Greenlaw 2020). Resulting swarms of SWD could have multiple effects on eastern towhee: annoy and deter birds by covering their eyes and heads while foraging on the ground (Forster 1979) or make fruits undesirable for consumption by covering them on the plant or among leaf litter where towhee forage. Meanwhile, hooded warbler may have been linked to declines of arthropod food resources in response to invasion by SWD (Adkins and Rieske 2013; Jennings et al. 2017). Invertebrates occur in greater abundances in early successional habitat compared to mature forest (Keller et al. 2003) and are an important food source for birds after the breeding season (Tietz and Johnson 2007; Diggs et al. 2011), affecting abundances (Buler et al. 2007; McDermott and Wood 2010). We did not assess fruit drop under *R. allegheniensis* plants, but any loss of fruits from plants may have reduced frugivorous and predatory foliage-dwelling arthropods (Sallabanks and Courtney 1992). Indeed, hooded warbler associate positively with invertebrate communities and, as a foliage-gleaning forager (Chiver et al. 2020), would be expected to decline in this scenario (McDermott and Wood 2010; Streby et al. 2011). Initial research has identified differences in invertebrate community composition in areas invaded by SWD (Bühlmann and Gossner 2022). Investigation into the direct and indirect impacts of SWD on invertebrate prey communities and why other species did not respond similarly to eastern towhee and hooded warbler is warranted.

Other than these two species, the songbird community in our regenerating timber harvests—as we defined frugivorous and non-frugivorous guilds, and the individual species within these guilds—showed no relationships to SWD. Despite this, it is clear SWD is present in large numbers and extensively parasitizes fruits of *R. allegheniensis*, one of the most common fruiting species and one of high value to vertebrate consumers (Martin et al. 1951). However, other variables were more important for predicting abundances of songbirds, notably cover and date (Table 4). Vegetation structure is often the most important habitat feature for predicting bird abundances following the breeding season (Vitz and Rodewald 2007; McDermott and Wood 2010). Our observed temporal relationships to date and large differences in captures of focal species between sampling rounds 1 and 2 reflect phenological patterns for many species in the region:

early migrants and timber harvest breeders declined, while later migrants and mature forest breeders accumulated over time. This suggests migration timing was the primary factor predicting most abundances. Many birds use a time-minimization strategy to reach overwintering grounds as quickly as possible (Hedenström 2008). Our lack of many recaptures suggests birds were using our sites for short amounts of time, which could have been insufficient to develop responses to SWD. As such, it may be more important to investigate year-round residents rather than migratory species.

Our results demonstrate an apparent resilience of the bird community to SWD. Invasive species can enter an existing ecosystem with little to no negative outcomes for that system (Sax et al. 2002). In this case, the next step is determining mechanistically how this community is resilient against SWD activity. Because we did not investigate fruit consumption or foraging by birds at our study sites, there is a need for direct observations of whether birds consume SWD-infested fruits. Parasitism does not guarantee fruit rejection by vertebrate consumers (Piper 1986; Valburg 1992a, b). Even if fruit parasitism by SWD reduces likelihood of fruit consumption, limitations in some food sources are often insufficient to alter habitat use (Alatalo 1980; Martin 1987). Birds are highly flexible in their diets, utilizing both fruit and non-fruit resources and altering foraging behaviors to meet energetic needs of migration (Loria and Moore 1990; Aamidor et al. 2011; McKinnon et al. 2017). Our observed lack of relationships to SWD may reflect plasticity of our birds to procure food resources, even if SWD altered fruit resources in regenerating timber harvests. This complements the relationships to date if plasticity allowed birds to reduce search time for suitable sites and utilize sites with different levels of resources, assuming foods were in enough supply to acquire necessary energy (Champlin et al. 2009).

However, presence alone does not always indicate habitat quality (Van Horne 1983). A lack of relationships of bird abundances to SWD could mask other possible responses to SWD. For example, multiple mechanisms—loss of fruit resources, direct consumption of SWD, indirect consumption through parasitized fruit, or alterations to invertebrate communities—may not affect abundances but instead reduce or provide new sources of nutrition (Piper 1986; Drew 1988), influencing energy expenditure while foraging, body condition, and ultimately migration success. Indirect techniques of diet analysis (e.g., metabarcoding) may help to elucidate this question of whether birds are consuming SWD.

Implementing studies of ecological consequences of SWD in natural systems will be challenging, especially those aimed at monitoring wildlife communities. Because SWD has been present in most of North America for a decade and is capable of rapid dispersal (Rota-Stabelli et al. 2013), locating uninvaded areas may be impossible without artificial exclusion. Comparing habitats across larger spatial extents will introduce more confounding factors. If monitoring in ecosystems has been ongoing, a temporally comparative study pre- and post-invasion may be possible. If wildlife are still developing responses to SWD due to the relatively recent introduction of SWD to the eastern United States (Watts et al. 2020), continued monitoring of SWD activity and wildlife communities now may provide opportunities to track responses to SWD invasion before more dramatic alterations to ecosystems occur. Internationally, SWD is still expanding its invaded range (Bieńkowski and Orlova-Bienkowskaja 2020; Kwadha et al. 2021). Opportunities exist outside the U.S. to study impacts of invasion of SWD on native wildlife and a variety of processes in ecosystems worldwide (Roche et al. 2021).

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Data availability All data used in this study are available from the corresponding author on reasonable request.

Code availability All code used in this study are available from the corresponding author on reasonable request.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval Capture and handling of birds described in this study was approved by the West Virginia University Animal Care and Use Committee under protocol 1904023217.

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