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Emerging Research

Invasion of Eastern Deciduous Forests by the Spotted Wing Drosophila: Impacts and Knowledge Gaps

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ABSTRACT Invasion of forest ecosystems by non-native invasive insect pests (NNIIPs) can alter native animal and plant communities by disrupting species interactions. However, little is known about how fruit-targeting NNIIPs may alter forest ecosystems. Recently introduced to the western United States, spotted wing Drosophila (*Drosophila suzukii*; SWD) is a parasite of soft-skinned fruits. The ability of SWD to parasitize still-ripening fruits of many plant species led to rapid expansion in agricultural systems across North America. Recent surveys have documented widespread SWD parasitism of wild fruits in forests, although impacts of parasitism remain unexplored. We investigated how SWD may produce ecological changes to eastern forests through several mechanisms: 1) disruption of plant–animal seed dispersal interactions; 2) subsequent alterations to plant community composition; and 3) changes in fruit consumption by wildlife. Parasitism of fruits by SWD may reduce attractiveness to potential seed dispersers, reducing overall consumption and shifting future plant communities away from fruit-producing species. Invasion by SWD may therefore have both short-term and long-term consequences for food resources for wildlife and ecosystem function. We highlighted frugivorous birds because of their importance as consumers and dispersers of fruits in eastern North America and their well-documented rejection of parasitized fruits. We proposed several critical avenues of research and call for a large-scale collaborative effort to understand the complex relationship SWD may play with plants and wildlife in forest ecosystems. © 2021 The Wildlife Society.

KEY WORDS *Drosophila suzukii*, frugivorous birds, fruit parasitism, fruit selection, invasive species, plant community composition, seed dispersal, species interactions, spotted wing Drosophila, trophic impacts.

Biological invasions can alter or interfere with interactions among species. Specifically, non-native, invasive insect pests (NNIIPs) in eastern North American forests can dramatically alter plant and animal communities (Table S1, available online in Supporting Information). Many species feed on plant material, ultimately increasing tree mortality and changing forest structure and plant community composition (Kenis et al. 2009, Brockerhoff and Liebhold 2017). Changes in forest structure affect wildlife species through modifications to microhabitat and microclimate characteristics (Kenis et al. 2009, Lovett et al. 2016, Brockerhoff and Liebhold 2017). Although impacts of NNIIPs on host plant mortality may be less pronounced at a regional scale, effects on plant mortality can be more acute at a local scale (Table S1; Davidson et al. 1999, Morin et al. 2015, Morin and Liebhold 2016, Fei et al. 2019). Thus, NNIIPs can influence entire ecosystems by feeding on plant foliage, sap, or wood of native plant species in North America.

However, many NNIIP species feed on fleshy fruits. Research has focused on the role of NNIIPs in agricultural systems where they can dramatically decrease cultivated fruit production (Clark and Gage 1997, Leskey et al. 2012). Many agricultural fields throughout eastern North America occur in forested landscapes, and forest cover promotes fruit-consuming NNIIPs in fruit crops (With 2002, Gardiner et al. 2009, Venugopal et al. 2014, Rice et al. 2017, Rodriguez-Saona et al. 2018). Non-crop host plants found in forests can play a critical role in maintaining fruit-consuming NNIIP populations (Bahlai et al. 2010, Rice et al. 2017, Rodriguez-Saona et al. 2018). Generalist

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NNIIPs are especially likely to benefit from non-crop host plants in forests (Rice et al. 2017). To date, however, little research has focused on fruit-consuming pests in forest ecosystems. As such, impacts of fruit-consuming NNIIPs on forest plant and wildlife communities remain poorly known (Kenis et al. 2017).

The spotted wing Drosophila (*Drosophila suzukii*, SWD) is a generalist NNIIP that is a potentially-damaging species, but presents an opportunity to understand how invasive fruit pests may impact forest ecosystems in eastern North America. Despite extensive research on SWD biology and ecology in connection with agricultural systems (Table S2, available online in Supporting Information), little is known about the connection of SWD to forest ecosystems by comparison. Because SWD parasitizes soft-skinned, fleshy fruits, this pest could affect several aspects of forest ecology: 1) fruit consumption by wildlife, 2) seed dispersal, 3) plant and wildlife community composition, 4) forest structure, and 5) ecosystem functions. Our objectives were to describe how parasitism of forest fruits by SWD may impact both plants and wildlife in forests and identify the potential implications of parasitism for future forest ecosystems. First, we provide background on SWD as a pest in agricultural systems. Second, we discuss the potential for disruption of seed-disperser relationships and implications for plant communities. Third, we discuss how wildlife may be impacted, with an emphasis on frugivorous birds because of their role as dispersers and well-documented responses to pest-induced damages to fruits. Finally, we propose several questions to guide initial research on the ecological impacts of SWD in forested ecosystems.

SPOTTED WING DROSOPHILA: A NOVEL PEST

Over the past decade, inadvertent introductions of SWD from its native range in east Asia have resulted in it becoming a significant global pest of many cultivated fruiting species, including berries (*Vaccinium* spp., *Rubus* spp.), grapes (*Vitis* spp.), and stone fruits (*Prunus* spp.; Lee et al. 2011, Walsh et al. 2011, Bellamy et al. 2013). In North America, SWD was first detected in 2008 in commercial fruit crops in California. Since initial detection, SWD has spread rapidly across the continent, apparently facilitated via shipped fruit (Rota-Stabelli et al. 2013), reaching Florida on the east coast by 2009, Michigan by 2010, and most northeastern states by 2011 (Hauser 2011). Similar rapid expansions of SWD have occurred in both Europe and South America at about the same time (Calabria et al. 2012, Cini et al. 2012, Deprá et al. 2014).

Unlike other fruit flies that feed on overripe or decaying fruit or other organic matter, female SWD have a hardened, serrated ovipositor that enables them to pierce the skin of ripening fruits to deposit eggs (Atallah et al. 2014). Emerging larvae destroy the fruit by consuming the flesh as they develop (Fig. 1); further loss often results from secondary pathogens that infect the fruit through oviposition incisions or premature fruit drop (Walsh et al. 2011). The females' preference for ripening fruit (Lee et al. 2011), coupled with the capacity of SWD for exponential population growth (Lee et al. 2011, Walsh et al. 2011, Kinjo et al. 2014, Tochen et al. 2014), makes SWD capable of enormous damage to commercial fruit crops.

In the United States, estimates of annual revenue losses from SWD-damaged fruit crops now exceed approximately $500 million in the Pacific Northwest and $200 million in the Northeast, in addition to expenses for intensified monitoring and pesticide treatments (Bolda et al. 2010, Goodhue et al. 2011, Burrack 2013, Farnsworth et al. 2017). Overall, losses in commercial fruit crop yield have ranged from estimates of negligible to 80% in the United States (Walsh et al. 2011), and recent surveys of berry growers estimate average national crop losses to SWD in 2014 from 6% in strawberries to 41% in raspberries (Burrack 2015). Losses in the eastern United States in cultivated blueberries and caneberries (*Rubus* spp.) ranged 0–30% and 10–80%, respectively (Burrack 2013). Thus, early reports suggest an

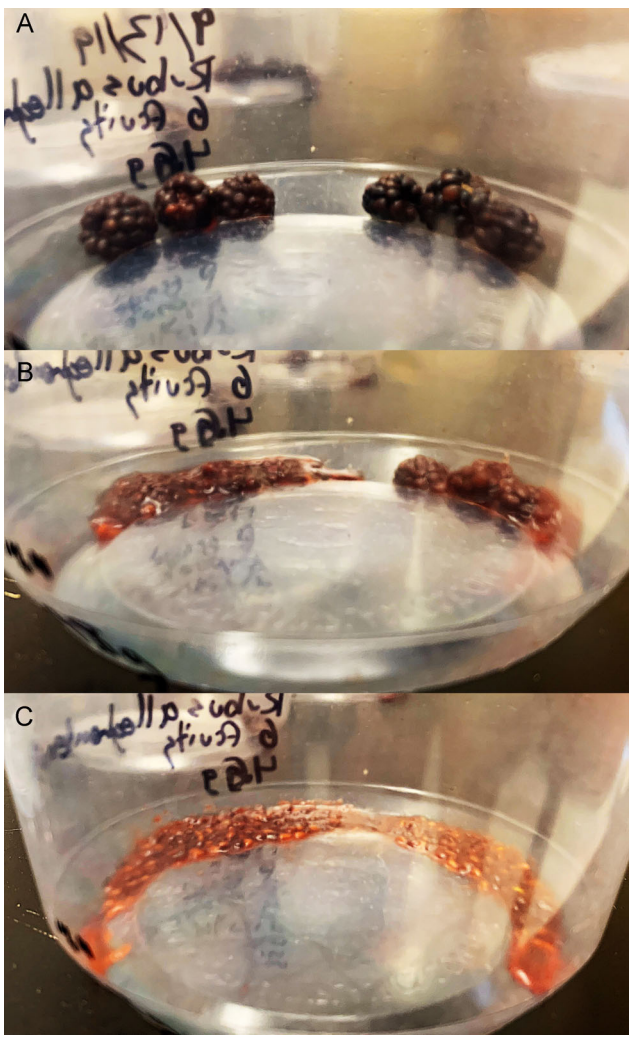

Figure 1. Allegheny blackberry (*Rubus allegheniensis*) fruits parasitized by spotted wing Drosophila (*Drosophila suzukii*). Fruits were collected in a regenerating timber harvest at Allegheny National Forest, Pennsylvania, in 2019. Pictures show the same fruit sample A) 2 days post-collection, B) 4 days post-collection, and C) 7 days post-collection.

important, widespread impact by SWD on fruit production in United States agricultural systems.

Many agricultural systems in the eastern United States occur in forested landscapes that might exacerbate or facilitate yield losses. As with many insect pests, greater forest cover and closer proximity of forest to croplands influence SWD in agricultural fields (With 2002, Gardiner et al. 2009). Abundance of SWD in agricultural land increased in blueberry orchards that were surrounded by more forest cover (Schmidt et al. 2019). Plant community composition in surrounding forests can promote the spread and increase abundance of SWD populations in agricultural landscapes by providing alternative food resources and acting as reservoirs for reinvasion (Klick et al. 2016). However, other than how forest cover affects SWD in nearby agricultural areas, data about the occurrence or impacts of SWD in forested systems are lacking.

POTENTIAL ECOSYSTEM IMPACTS

In North America, SWD has been found in forests surrounding agricultural lands parasitizing the fruits of wild plants (Walsh et al. 2011, Lee et al. 2015, Ballman and Drummond 2017). To date, more than 100 plant species worldwide have been identified as viable hosts for SWD, including many wild taxa (Lee and Sial 2016). In the United States, numerous native and non-native plants bearing soft-skinned fruits have been documented as hosts of SWD, including brambles (*Rubus* spp.), cherries (*Prunus* spp.), honeysuckles (*Lonicera* spp.), blueberries and huckleberries (*Vaccinium* and *Gaylussacia* spp.), dogwoods (*Cornus* spp.), elderberries (*Sambucus* spp.), pokeweed (*Phytolacca* spp.), buckthorns (*Rhamnus* and *Frangula* spp.), and nightshades (*Solanum* spp.), among others (Table S3, available online in Supporting Information).

Fruits are used by plants as an attractant to vertebrate seed dispersers, including many birds and mammals (Ridley 1930, Van der Pijl 1972, Herrera 1982, Sallabanks and Courtney 1992). Because many plants rely on vertebrate dispersers to transport seeds to germination sites for recruitment, fruits provide a nutritional reward, incentivizing dispersers to consume fruits (Snow 1971, McKey 1975, Sallabanks and Courtney 1992). Further, fruits of many plants possess traits to effectively attract dispersers, including coloration, scent, size, or accessibility on the plant (Van der Pijl 1957, Snow 1971, Willson and Thompson 1982, Willson 1993). By directly targeting reproductive tissues of wild fruit-producing plants, frugivorous insects like SWD may inhibit plant seed dispersal in forests, though the effects of SWD larvae on fruit seed viability remain unknown.

Insects can disrupt plant–disperser relationships by altering the attractiveness of fruits. Insect pests can inhibit the maturation of fruit, stopping color change that vertebrate seed dispersers cue in on to select fruits for consumption (Jordano 1987, Krischik et al. 1989, Traveset 1993). Parasitism of fruits by insect larvae can change other fruit traits, including the texture (Carter 1939), size, and shapes of fruits (Highland 1964). Attack by insect pests can also expose fruits to microbial or fungal infection, making them less palatable to potential dispersers (Manzur and Courtney 1984, Jordano 1987, Borowicz 1988, Traveset et al. 1995, García et al. 1999). Indeed, vertebrate consumption of fruits often decreases when fruits are parasitized by insect pests (Sallabanks and Courtney 1992). Janzen (1971) found that rodents reject fruits of a legume tree (*Cassia grandis*) parasitized by moths, and Engriser (1995) found that phyllostomid bats (*Sturnia ludovici*, *Carollia brevicauda*) select against fruits of a small shrub-tree (*Acnistus arborescens*) parasitized by insect larvae in early successional habitats. Frugivorous birds will discriminate against blueberries based on changes to fruit shape caused by moths (i.e., *Lotisma trigonana*) and sawflies (i.e., *Melastola resincolor*; Traveset et al. 1995). Similarly, blackbirds (*Turdus merula*) will reject hawthorn (*Crataegus monogyna*) fruits parasitized by insects based on color and palatability changes, resulting in failure to ingest and disperse the seeds of up to 15% of the healthy fruit crop (Manzur and Courtney 1984). Parasitism of fruits is likely to be most detrimental for seed dispersal if important dispersers refuse to consume parasitized fruits.

However, fruit parasitism by insects might produce no change to avian consumption (Piper 1986, Nalepa and Piper 1994). Valburg (1992*a*,*b*) even reported discrimination in favor of fruits containing pulp-eating insects. Others have suggested parasitism makes fruit more attractive to avian frugivores (Webber and Woodrow 2004), in that insect larvae within the fruit increase the palatability, levels of secondary compounds, or protein content of the fruit and make the fruit more rewarding (Piper 1986, Drew 1988). Despite potential benefits of insect parasitism on avian fruit consumption in some contexts, widely observed selection against parasitized fruits suggests a decrease in fruit resource consumption for at least some frugivorous birds in response to SWD. Foraging birds will leave as much as 75% of insect-parasitized fruits on a plant (Burger 1987), which might mask and reduce the consumption of healthy fruits. Birds select plants for foraging based upon traits including fruit size and pulpiness (Sallabanks 1993), which might further explain the failure to remove all healthy fruits from plants with many parasitized fruits. Further, experimental reduction of fruit decreases the local abundance of frugivorous birds (Moegenburg and Levey 2003, Major and Desrochers 2012). Soft fruits are clearly a critical resource, and alterations to abundant fruit resources for consumption due to insect parasitism could have negative consequences for wildlife (Table 1).

Frugivorous birds play a critical role as seed dispersers for many fruiting plants (Thompson and Willson 1979; Snow and Snow 1988; García et al. 2010, 2011). They may disperse seeds of up to 40% of woody plant species in temperate forests (Jordano 2000, Herrera 2002). In eastern North America, birds serve as the primary seed dispersers for most plants bearing soft fruits and can consume up to 80% of a standing fruit crop (Baird 1980, Willson 1986). Further, processing of fruit in the gizzard, stomach, or gut

Table 1. Summary of potential impacts of spotted wing Drosophila (*Drosophila suzukii*) invasion in forested ecosystems.

Immediate impact	Ecosystem impacts	Wildlife impacts
Parasitism of forest fruits	Reduced attractiveness of fruits to wildlife (i.e., dispersers)	Loss of fruit resources
	Reduced fruit consumption by dispersers	Reduced capacity for larger populations
	Reduced seed dispersal	
	Reduced recruitment of fruit-producing species	Increased competition for fewer food resources
	Fewer fruits	Reduced energy intake
	Plant community composition shift	Diet switching to alternative resources
	Reduced diversity	Reduced survival
	Shift in forest structure	Reduction in desired habitat structure
	Carbon storage, nutrient cycling, natural restoration ability changes	Loss of frugivores
	Altered forest community	
	Ecosystem function, resilience decline	

often increases the probability of subsequent seed germination (Traveset and Verdú 2002, Fricke et al. 2013). Seed deposition by birds can strongly influence patterns of plant regeneration and therefore plant community composition (Howe and Smallwood 1982, McDonnell and Stiles 1983, Caves et al. 2013). Over time, reductions in frugivorous birds due to SWD may lead to shifts in plant communities away from fruit-producing species (Matlack 1994). Changes to the plant community may lead to changes in carbon storage, nutrient cycling, and natural restoration capacity (Lovett et al. 2016), and ultimately to declines in ecosystem function (Farwig and Berens 2012) and resilience (Table 1; Gunderson 2000, Folke et al. 2004).

POTENTIAL WILDLIFE IMPACTS

Fruit parasitism by SWD may create direct competition with wildlife for fruit, leading to reduced food resources, increased competition for remaining fruit and alternative food resources, and subsequent declines in wildlife populations (Table 1). Many documented plant hosts of SWD occur in the understories of forests (Table S3). Reduced dispersal of plant hosts may alter understory vegetation structure, especially if replaced with species that produce inhibiting vegetation layers (Horsley and Marquis 1983, Horsley 1986, Baumer and Runkle 2010). Changes to structure may influence suitability for wildlife such as songbirds (Rodewald and Smith 1998, Bell and Whitmore 2000, Matsuoka et al. 2001), wild turkey (*Meleagris gallopavo*; Metzler and Speake 1985), ruffed grouse (*Bonasa umbellus*; Jones et al. 2008), small mammals (Carey and Johnson 1995), and amphibians (deMaynadier and Hunter 1995). Reduced dispersal of fruit may also reduce future resources as fruit-producing species are replaced by non-fruit-producing species in the community, furthering frugivore reductions.

In eastern North America, soft fruits provide a critical food resource for many wildlife species (Martin et al. 1961, McCarty et al. 2002), including many migratory birds such as *Catharus* thrushes (Family: Turdidae) and waxwings (Family: Bombycillidae) and mammals such as American black bear (*Ursus americanus*) and fisher (*Pekania pennanti*; Willson 1986, Parrish 1997, Inman and Pelton 2002, McNeil et al. 2017). Abundant soft fruits increase American black bear productivity and survival (Rogers 1976, Eiler et al. 1989) and decrease wild turkey harvests because turkeys spend less time foraging, thus reducing exposure to hunters (Ryan et al. 2004). Many soft fruit species ripen in the fall, providing a highly nutritious, valuable fruit resource to many vertebrates, including white-tailed deer (*Odocoileus virginianus*), white-footed mice (*Peromyscus leucopus*), game birds (e.g., wild turkey, ruffed grouse), mesocarnivores (e.g., red fox [*Vulpes vulpes*], raccoon [*Procyon lotor*], squirrels [Family: Sciuridae]), and American black bears (Uchytil 1991, Ryan et al. 2004, Rose et al. 2014). Because many songbird species shift from a completely insectivorous diet during the breeding season to include substantial amounts of fruit after breeding, in migration, and over winter (Fuentes 1994; Parrish 1997, 2000; Suthers et al. 2000), bird abundance varies with soft fruit abundance in the post-breeding and migration periods (Baird 1980, Rodewald and Brittingham 2004, Gleditsch and Carlo 2011, Major and Desrochers 2012).

Potential reductions in fruit consumption due to SWD might be especially damaging to populations of frugivorous forest birds. Avian frugivore abundance and foraging behavior are positively correlated with fruit availability in many different regions, including tropical forests (Levey 1988, Loiselle and Blake 1991, Saracco et al. 2004), temperate European forests (Plein et al. 2013), and temperate North American forests (McCusker et al. 2010). Frugivorous birds will also respond directly to changes in abundance of fruit resources. Two frugivorous birds, Eurasian blackcap (*Sylvia atricapilla*) and song thrush (*Turdus philomelos*), respond to human harvesting of olive fruits in Spanish olive orchards by redistributing to unharvested patches (Rey 1995). In mature longleaf (*Pinus palustris*) and loblolly (*Pinus taeda*) pine stands in the southeastern United States, yellow-rumped warbler (*Setophaga coronata*) abundance increases when southern wax myrtle (*Myrica cerifera*) fruit increases during the winter (Borgmann et al. 2004). In temperate ecosystems, many bird species rely on nutrient- and energy-rich fruit resources as a valuable dietary component for at least part of the year (Thompson and Willson 1979, Howe and Smallwood 1982, Suthers et al. 2000, Major and Desrochers 2012). Consumption of soft fruits aids in building energy reserves (Snow 1971, Martin 1985, Parrish 1997, Schaub and Jenni 2000). Without these vital fruit resources, frugivorous birds might fail to build and maintain sufficient energy stores, increasing mortality at certain times of year (Parrish 2000). Thus, there

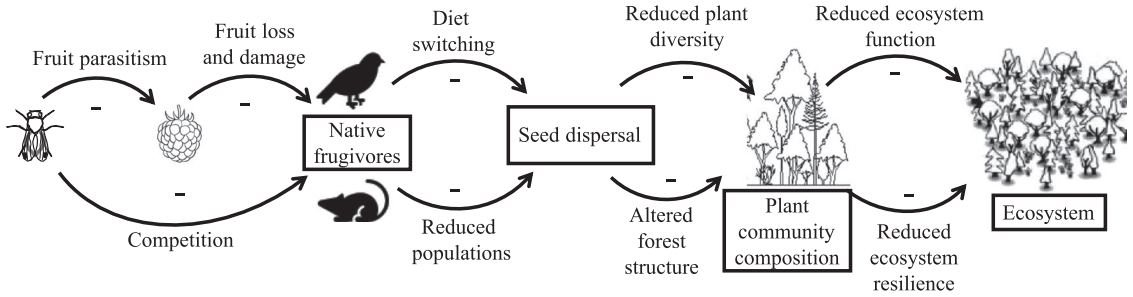

Figure 2. Potential ecological interactions and trophic consequences of fruit parasitism by spotted wing Drosophila (*Drosophila suzukii*, SWD) in eastern forests of North America. Arrows indicate directions of interactions and signs indicate negative consequences of the effect. Loss of fruit to SWD will reduce fruit available for vertebrate frugivores, forcing wildlife to find alternative food resources and potentially reducing their populations. Diet switching and loss of frugivores will disrupt seed dispersal and ultimately reduce plant diversity, alter forest structure, and impede ecosystem function and resilience.

are numerous potential ecological interactions and consequences of fruit parasitism by SWD in eastern forests of North America (Fig. 2).

RESEARCH NEEDS IN EASTERN FORESTS

The impacts of SWD on native ecosystems may be indirect through the cascading effects of altered seed dispersal, plant regeneration, and fruit loss on wildlife populations. Impacts may also be through direct exploitative competition with native frugivores. Indirect effects of biological invasions are often neglected in studies of invasive species, yet may have varied and long-term consequences (White et al. 2006). The potential for significant short- and long-term changes to eastern forest ecosystems from frugivorous NNIIPs requires greater investigation.

There are some unresolved questions regarding the role of SWD in forest ecosystems. Basic information about SWD distribution, abundance, and phenology in forest ecosystems are lacking. Thus, research focused on understanding the limiting factors affecting SWD distribution will be imperative for guiding broader ecological questions and developing mitigation or control strategies.

Information on damage levels to forest fruits are similarly lacking. While extensive damage may be inferred from agricultural research and surveys around croplands for some species (Lee et al. 2015, Ballman and Drummond 2017), fruiting forest plants may avoid extensive damage through mast seeding, or masting (Kelly and Sork 2002). By intermittently synchronizing large production of fruits, plants can overwhelm fruit or seed predators (predator satiation hypothesis; Janzen 1971, Silvertown 1980). Overwhelming fruit or seed predators reduces loss of fruits to parasitism and causes predator populations to cycle with frequency of masting (Satake et al. 2004). If masting species are present, they may reduce parasitism of forest fruits of the same species and other species susceptible to SWD, especially those other susceptible species that synchronize masting (Shibata et al. 1998, Kelly et al. 2000). However, generalist host use by SWD suggests negative impacts of possible masting on SWD population cycles may be dampened (Satake et al. 2004). In the absence of masting, actual parasitism rates by SWD may affect different species drastically or at a low enough magnitude to be considered insignificant. Thus, it will be critical to survey damage levels to fruits of different forest plant species in different regions to understand broader ecological impacts of SWD on plants and wildlife.

Broader ecological questions about SWD can focus on addressing knowledge gaps related to other ecological relationships. For instance, how does parasitism affect fruit selection or rejection by different vertebrate dispersers, and do vertebrate dispersers respond differently? Or, does parasitism affect the viability of seeds in those fruits? Does that viability vary among fruiting species? Many known host species of SWD are invasive in North America (Table S3). An invasive species can impede or enhance the impacts of another invasive species on an ecosystem (Agrawal et al. 2005, Simberloff 2006). If parasitism impacts fruit selection or seed viability, could SWD disrupt or promote the dispersal of invasive fruiting plants by native frugivores? Reciprocally, could invasive plant species disrupt or promote dispersal of SWD (Engelkes and Mills 2013)? And how does SWD interact with resident predators (vertebrate and invertebrate) and parasitoids in forests? Resident predators and parasitoids can aid in suppressing SWD in crop systems (Lee et al. 2019), and efforts are currently being researched to promote hummingbirds, a known predator of fruit flies, in crop fields using feeders as a form of management (J. Carroll, Cornell University, personal communication). Answering these questions is imperative to understanding potential impacts to plant regeneration and composition of future forest plant and wildlife communities.

Similarly, because ecosystem impacts of SWD invasion may not be obvious in the short-term, long-term monitoring of forest plant communities will be critical to identifying whether changes occur in response to continued SWD activity. Unfortunately, evidence suggests that SWD are present throughout much of the eastern forests, so designing experiments to compare invaded vs noninvaded areas will be problematic. Instead, monitoring potential changes in regenerating forest community composition can provide insights into long-term effects. Wildlife community responses can also be prioritized, considering shifting forest tree species composition and effects of SWD on soft-fruit food resources. Long-term wildlife monitoring will provide

information about any lasting ecological effects of SWD on wildlife populations. The broad scope of potential impacts calls for a focused, multi-disciplinary research effort to study SWD in forests. Collaboration between forest managers, wildlife biologists, entomologists, plant ecologists, and other relevant fields will be critical to understanding the complex relationship SWD may play with plants and wildlife in forest ecosystems.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's web-site. This material contains examples of impacts of non-native invasive insect pests on forested ecosystems in the eastern United States, existing research topics on spotted wing Drosophila (SWD) represented in literature, and a list of documented non-crop fruit hosts of SWD in North America.