

Before the Secretary of the Interior

Petition to list

the mysterious lantern firefly

***Photuris mysticalampas* Heckscher, 2013**

as an endangered species

under the U.S. Endangered Species Act



Photo by: Radim Schreiber (fireflyexperience.org)

Submitted by

The Xerces Society for Invertebrate Conservation

Prepared by Emily Geest, Sharon Selvaggio, and Candace Fallon

March 14, 2023

NOTICE OF PETITION

Deb Haaland, Secretary
U.S. Department of the Interior
1849 C Street NW
Washington, D.C. 20240
exsec@ios.doi.gov

Martha Williams, Director
U.S. Fish and Wildlife Service
1849 C Street NW
Washington, D.C. 20240
Martha_Williams@fws.gov

Gary Frazer, Assistant Director
U.S. Fish and Wildlife Service
1840 C Street NW
Washington, D.C. 20240
Gary_Frazer@fws.gov

Wendi Weber, Director
Region 5 U.S. Fish and Wildlife Service
300 Westgate Center Drive
Hadley, MA 01035-9589
Wendi_Weber@fws.gov

PETITIONER

The Xerces Society for Invertebrate Conservation is a nonprofit organization that protects wildlife through the conservation of invertebrates and their habitat. For fifty years, the Society has been at the forefront of invertebrate protection worldwide, harnessing the knowledge of scientists and the enthusiasm of citizens to implement conservation programs. Xerces is a leader in firefly conservation, working with partners to better understand the distributions of vulnerable species through a [Firefly Atlas](#), assess the extinction risk of North American species, identify and implement priority conservation actions, and engage land managers, policymakers, researchers, and the public in their protection.

The Honorable Deb Haaland
Secretary, U.S. Department of Interior
1849 C Street, NW Washington, DC 20240

Dear Secretary Haaland,

Pursuant to Section 4(b) of the Endangered Species Act (“ESA”), 16 U.S.C. § 1533(b); Section 553(e) of the Administrative Procedure Act, 5 U.S.C. § 553(e); and 50 C.F.R. § 424.14(a), the Xerces Society for Invertebrate Conservation hereby petitions the Secretary of the Interior, through the United States Fish and Wildlife Service (“FWS,” “Service”), to protect the mysterious lantern firefly (*Photuris mysticalampas* Heckscher, 2013) under the ESA as an endangered species. Petitioner also requests that critical habitat be designated for the firefly concurrently with the listing, pursuant to 16 U.S.C. § 1533(a)(3)(A) and 50 C.F.R. § 424.12.

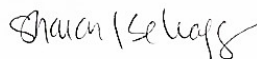
Fireflies are charismatic animals that have long inspired the human psyche. Recent research has revealed that a number of North American species are at risk of extinction, due to threats including habitat loss and degradation, climate change, and light pollution. The mysterious lantern firefly, a native species endemic to the Delmarva Peninsula of Delaware and Maryland, is associated with high quality forested peatland floodplain habitats. It is known from only six sites in two watersheds—the Nanticoke watershed and the Broadkill-Smyrna watershed—although the status of the population in the Broadkill-Smyrna watershed is uncertain. As a habitat specialist, the mysterious lantern firefly is threatened by habitat loss, fragmentation, and degradation. It is not known to disperse very far, and its nocturnal courtship behavior makes it especially vulnerable to light pollution. Sea level rise and increased storm surges along the Atlantic Coast are a threat to this species, as is widespread pesticide use and the spread of invasive plants throughout its habitat. Despite dedicated search efforts, this firefly has been found in only a few sites. Furthermore, existing regulatory mechanisms are inadequate to protect this species from extinction.

We recognize that this petition sets into motion a specific process placing definite response requirements on the Service and very specific time constraints upon these responses 16 U.S.C. § 1533(b). We will therefore expect a finding by the Service within 90 days regarding whether our petition contains substantial information to warrant a full status review.

Sincerely,



Emily Geest



Sharon Selvaggio



Candace Fallon

The Xerces Society for Invertebrate Conservation

628 NE Broadway | Suite 200 | Portland, OR, 97232-1324, USA | 503-232-6639

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Executive summary

The mysterious lantern firefly, *Photuris mysticalampas*, is a rare, range-restricted firefly species first described by Dr. Christopher Heckscher in 2013. It is known only from the Delmarva Peninsula along the Atlantic coast of the U.S., where it has been documented from just six sites in Delaware and Maryland. This nocturnal, flashing species is a habitat specialist, occurring within high quality forested floodplains in the Nanticoke and Broadkill-Smyrna watersheds. It can be distinguished from other *Photuris* fireflies in its range by its comparatively small oval shaped body and a distinctive, prolonged green-yellow flash that inspired its name.

Five of the sites where this species is known to occur are located within approximately 14 miles of each other on state wildlife area and Nature Conservancy lands along the Maryland-Delaware border. The sixth, disjunct site, is located nearly 18 miles away to the northeast along the Atlantic coast in the Prime Hook National Wildlife Refuge. A recent survey at this site did not result in any detections of the species, suggesting the population may no longer be extant. If so, the known extent of occurrence for this species would be much reduced.

The mysterious lantern firefly is imperiled by multiple threats including habitat fragmentation, pesticide use, climate change, light pollution, small population size, recreation, invasive species, and a lack of protective regulatory mechanisms, among other factors. While this species has been recorded on federal, state, and private conservation lands, there are no species-specific management activities aimed at protecting this species. Additionally, the passive protection allotted from these managed areas cannot protect this species from new and emerging threats including sea level rise and increased frequency and severity of storms that can destroy or degrade the forested peatlands upon which this firefly depends. In sum, the mysterious lantern firefly is particularly threatened by ESA listing factors 1 (modification or curtailment of habitat or range), 4 (inadequacy of existing regulatory mechanisms), and 5 (other natural or manmade factors affecting this firefly's continued existence), although all five factors (including factor 2, overutilization, and factor 3, disease or predation) may be impacting the species.

Accordingly, we hereby request that the Service list the mysterious lantern firefly (*Photuris mysticalampas*) as an endangered species. Once listed, we recommend that the Service permit activities that promote the conservation of the species, such as scientific research and monitoring, community science monitoring, and limited collection for research and identification purposes.

Introduction

Fireflies are highly charismatic beetles revered among the public with significant cultural (Bascom 1979; Schuettler 2007; Lewis 2016; Faust 2017; Lewis et al. 2020), biological (Woods Jr. et al. 2007; Bauer et al. 2013; Oba & Schultz 2022), and economic importance (Bauer et al. 2013; Lewis 2016; Lewis et al. 2020). Fireflies are often associated with summer nights (Lewis 2016), and viewing fireflies is a pastime shared around the world (Laurent & Ono 1999; Faust 2010; Vance & Kuri 2017). Recreational viewing of fireflies is growing significantly globally, bringing fireflies even further into the public's attention (Faust 2010; Vance & Kuri 2017; Lewis et al. 2021).

Fireflies belong to the order Coleoptera and can be found on every continent except Antarctica (Lewis 2016). Globally, there are over 2,000 species of fireflies (Coleoptera: Lampyridae), with at least 170 of these species residing in North America, classified into 4-5 subfamilies and 16 genera (Stanger-Hall et al. 2007; Faust 2017; Lloyd 2018; Heckscher 2021; Ferreira et al. 2022). Only some genera exhibit the characteristic flashing as adults, but larvae of all known species produce light (Faust 2017). Firefly larvae use bioluminescence to warn predators of unpalatable steroids they contain (Underwood et al. 1997). Firefly adults use bioluminescence as a form of mate communication (Faust 2017). In the United States, fireflies can thus be categorized into three distinct groups based on their communication behavior: the flashing fireflies, the glow-worms, and the daytime dark fireflies, which are non-luminescing as adults and are diurnal species (Faust 2017).

Fireflies, like many insect groups, have undergone population declines globally in the past few decades (Khoo et al. 2009; Wong & Yeap 2012; Lewis 2016; Lewis et al. 2020), prompting firefly researchers at the 2010 International Firefly Symposium in Selangor, Malaysia, to sign the Selangor Declaration, a document that calls for urgent action to conserve fireflies (Fireflyers International Network 2014). Causes of firefly decline are thought to include loss of habitat (De Cock 2009; Lewis et al. 2020; Gardiner & Didham 2020), water pollution (Lewis et al. 2020), pesticides (Lewis et al. 2020), commercial harvesting (Bauer et al. 2013; Lewis et al. 2020), and light pollution (Owens & Lewis 2018; Thancharoen & Masoh 2019; Mbugua et al. 2020), among others.

Recent assessments of North American fireflies have revealed that up to a third of US species may be at risk of extinction, and approximately half of the assessed species are so poorly understood that they have been classified as data deficient (Fallon et al. 2021). The mysterious lantern firefly (*Photuris mysticalampas*) is one of these at-risk species. Assessed as Endangered by the IUCN Red List of Threatened Species (Fallon & Heckscher 2021), it is one of 64 described species of *Photuris* in the United States (Lloyd 2018; Faust & Davis 2019; Heckscher 2021). It is one of only two firefly species endemic to the Delmarva Peninsula (the other being the Bethany Beach firefly, *Photuris bethaniensis*, which is currently under review for ESA listing), occurring within a single county in Delaware (Fallon & Heckscher 2021) and a single county in Maryland (Firefly Atlas 2022). The habitat that the mysterious lantern firefly uses—high-quality forested peatland floodplains—was once abundant across the peninsula, but now occurs in remnant patches that are further threatened by sea level rise and increased storm surges from

climate change (Fallon & Heckscher 2021). Light pollution, pesticide use, and introduced plants also threaten this species and its habitat. The loss of this species would be a tremendous loss to science and our ability to study fireflies, their evolution, behavior, bioluminescence, and adaptations to their environments and to climate change. In addition, this species, as all species, has inherent value and a right to exist that is codified into U.S. law by the Endangered Species Act. Without ESA protection, we will lose this species to extinction, and with it, an important element of the Delmarva Peninsula’s biodiversity.

Conservation status and listing history

The mysterious lantern firefly (*Photuris mysticalampas*) has no legal protection under the U.S. Endangered Species Act or any state endangered species statutes. To our knowledge, it has never been petitioned for listing under the Endangered Species Act and it has no other federal status. NatureServe (2023) ranks this species as G1G2 (Critically Imperiled) throughout its range. It has not been ranked at the national or state level (NatureServe 2023). The International Union for Conservation of Nature ranks the species as Endangered (Fallon & Heckscher 2021; Fallon et al. 2021). The mysterious lantern firefly is also listed as a Species of Greatest Conservation Need (SGCN) in Delaware (Delaware Division of Fish and Wildlife 2015). Although Maryland also includes fireflies as SGCN (Maryland Department of Natural Resources 2015), this species is not listed, as it was not known to occur in the state until 2022.

Natural history

Taxonomy

The mysterious lantern firefly, *Photuris mysticalampas*, is a beetle in the order Coleoptera. It was first recognized as a distinct taxon in 2005 and later formally described by Christopher M. Heckscher in 2013. It is considered a valid species with no known subspecies (Heckscher 2013; ITIS 2023; Table 1). Unlike other species of *Photuris*, which are difficult to distinguish from one another morphologically and are often placed into species complexes, *P. mysticalampas* has morphological characters—a small, oval-shaped body when viewed from above and densely pubescent elytra—that clearly distinguish it from other species within its range (Heckscher 2013; Lloyd 2018). The oval body outline is rather pronounced, with a large width-to-length ratio; other *Photuris* species in the area have a more slender body shape (Heckscher 2013).

Table 1. Taxonomy of *Photuris mysticalampas*

Taxonomic Level	Taxonomic Designation
Order	Coleoptera
Superfamily	Elateroidea
Family	Lampyridae
Subfamily	Photurinae
Tribe	Photurini
Genus	<i>Photuris</i>
Species	<i>Photuris mysticalampas</i>

Description

Adult mysterious lantern fireflies can be distinguished from other fireflies in their range by a small oval shaped body, dense elytral pubescence, specific habitat association, and unique flash pattern (Heckscher 2013 p. 93; Lloyd 2018 p. 255; Figure 1). At 8.2-10.55 mm in length, adults are considered small for the genus (Heckscher 2013). The elytra (modified, hardened forewings found in beetles) range from light brown to gray and the thorax is typically brown (Heckscher 2013 p. 94). Its flash pattern consists of a medium luminosity single flash, generally appearing more green than yellow (Heckscher 2013 p. 98). Each flash is unusually prolonged (0.4-0.8 seconds, occasionally longer than 1 second) which is how mysterious lantern fireflies received their name. Occasionally, females have been known to give multiple weak flashes when signaling to males and males give trembling flashes when quickly approaching females (Heckscher 2013 p. 98).



Figure 1. Dorsal (left and center) and ventral (right) images of the mysterious lantern firefly, *Photuris mysticalampas*. Pinned specimen image (holotype) on left by Christopher M. Heckscher. Center and right photos by Candace Fallon/Xerces Society.

Range and population status

The mysterious lantern firefly occurs on the Delmarva Peninsula in Delaware and Maryland. It was first recognized as a distinct taxon in 2005 and later formally described in 2013 from the Nanticoke River floodplain in Sussex County, Delaware (Heckscher 2013). Additional individuals were collected from the original type locality and a second nearby site in 2005, 2008, 2010, and 2011 (Heckscher 2013). Another individual, collected in 2004 from Prime Hook National Wildlife Refuge (NWR), was also later determined to be this species (Heckscher 2013). All individuals collected prior to the species description originated from these three localities in Sussex County, Delaware. Two additional localities, also within the Nanticoke River floodplain, were later discovered (C. Heckscher pers. comm. 2023).

Survey efforts in 2022 resulted in the first documented Maryland locality and the sixth site overall for this species, also located within the Nanticoke River floodplain (Firefly Atlas 2022). The mysterious

lantern firefly is now known from six sites in four locations (Table 2, Figure 2). However, while the Nanticoke River floodplain sites are all thought to be extant, the status of the Prime Hook NWR site is uncertain; a brief revisit in 2011 failed to detect the species (Fallon & Heckscher 2021; C. Heckscher pers. comm. 2023). This species has not been found in similar habitat in New Jersey despite limited survey effort, nor has it been found in seemingly suitable habitat north of known localities in Delaware (NatureServe 2023) or further south along the Pocomoke River in Worcester County, Maryland (C. Fallon pers. obs. 2022, C. Heckscher pers. comm. 2023).

Table 2. All known sites of *Photuris mysticalampas*. A separate file with locality data will be provided to the Service at the time of submission.

Location	No. of sites	Land manager	County	State	Date last observed	Current Population Status	Reference
Prime Hook NWR	1	US Fish and Wildlife Service	Sussex	DE	July 2, 2004	Uncertain	Heckscher 2013; C. Heckscher pers. comm. 2023
Nanticoke State Wildlife Area	3	Delaware Department of Natural Resources and Environmental Control	Sussex	DE	June 2022	Extant	Heckscher 2013
Middleford North Preserve	1	The Nature Conservancy	Sussex	DE	July 21, 2021	Extant	C. Heckscher pers. comm. 2023
Nanticoke Preserve	1	The Nature Conservancy	Wicomico	MD	July 10, 2022	Extant	Firefly Atlas 2022

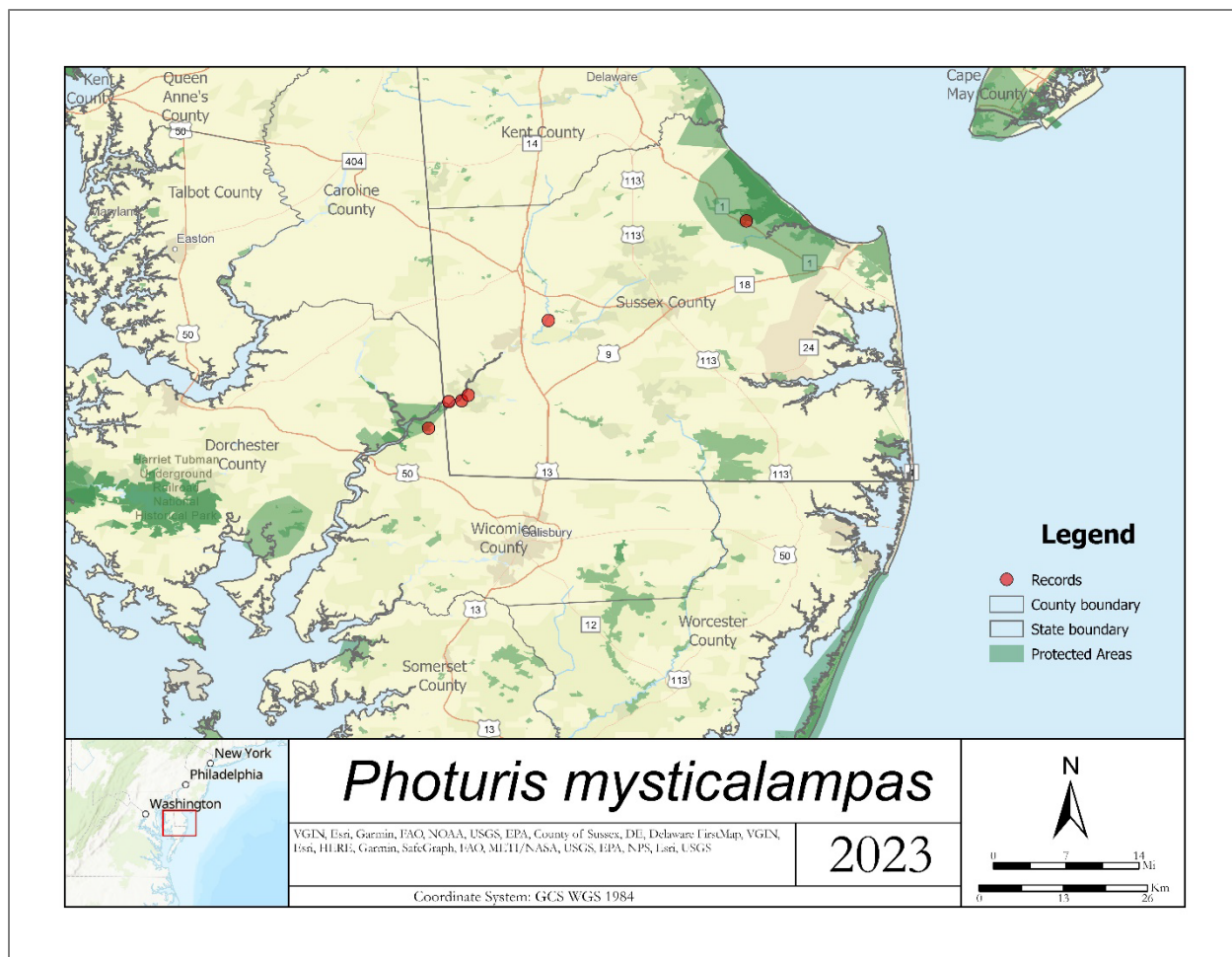


Figure 2. Map of *Photuris mysticalampas* distribution on the Delmarva Peninsula of Maryland and Delaware.

Population size and structure

No monitoring programs are in place for this species, so detailed data on population size, trend, and abundance are not available. However, the population trend is suspected to be declining due to widespread habitat loss and degradation (see the discussion of Factor 1 under Current and potential threats – An assessment of factors). This species has a very small range and is known from only six sites in two counties (Heckscher 2013; Firefly Atlas 2022; C. Heckscher pers. comm. 2023). Given the patchy distribution of its forested peatland habitat, it is likely that population connectivity is low. Where it does occur, it can be locally abundant; Faust (2017 p. 227) notes that “large groups of over one hundred males drift as they silently display...”

Life cycle and behavior

The mysterious lantern firefly is a beetle with a holometabolous life cycle, meaning it undergoes four stages of life: egg, larva, pupa, and adult. Female fireflies will lay an average of 28 eggs, typically a few at a time over multiple days to weeks (Faust 2017; Lloyd 2018). Eggs will hatch a few weeks after being laid (Faust 2017). Generally, fireflies will spend the majority of their lifetime (1-2 years) as larvae, undergoing

4-7 growth stages called instars (Faust 2017; Lloyd 2018). *Photuris* larvae are generalist predators consuming worms, slugs, snails, and other soft-bodied invertebrates (Faust 2017). Both firefly larvae and their soft-bodied prey are reliant on moisture as they can easily desiccate (Faust 2017). Larvae pupate in constructed chambers under the soil surface or under logs and emerge as adults a few weeks later (Faust 2017; Lloyd 2018). Adult fireflies typically do not eat, with the exception of *Photuris* spp. females (including those of *P. mysticalampas*) that will mimic other fireflies, to lure them in as prey (Faust 2017 pp. 181, 229). These females will then sequester protective toxins called lucibufagins that they have acquired from their prey and pass these toxins on to their young as a protective measure (Faust 2017). Some adult species have also been observed consuming plant material including berries, milkweed nectar, and apple slices (Buschman 1984; Faust 2017). Adult *Photuris* typically live 3-4 weeks and are active after dark during the summer months (Faust 2017); all known observations of the mysterious lantern firefly have occurred in June and July (Heckscher 2013; Faust 2017; Firefly Atlas 2022).

Both male and female mysterious lantern fireflies flash (Heckscher 2013). Courtship flashes are unique to each species—this species is characterized by a single prolonged flash, appearing more green than yellow (Heckscher 2013). Courtship signaling begins around 28-30°C (82-86°F) (Heckscher 2013). Males exhibit a single flash that lasts usually between 0.4-0.8 seconds, every 3-7 seconds (Heckscher 2013). However, sometimes the signal can exceed 1.0 second and the interval between signals can be longer than 7 seconds (Heckscher 2013). The flash is considered to be of medium luminescence for a *Photuris* species (Heckscher 2013). Occasionally, females will give short weak flashes when signaling to males, and when males approach a female, a trembling green flash may be given (Heckscher 2013). Adults emerge 30-40 minutes after sunset and can remain active until past midnight (Heckscher 2013; Faust 2017), with males patrolling the understory at low levels (<2m) (Heckscher 2013). Similarly, females remain low (<1m) on vegetation when signaling to males (Heckscher 2013).

Habitat

The mysterious lantern firefly is a habitat specialist dependent on palustrine (swampy) forested wetlands. Although the majority of Delaware's freshwater wetlands are considered palustrine forested wetlands (Tiner 2001 p. 6), this species is only found in high quality forested peatland floodplains, where Atlantic white cedar (*Chamaecyparis thyoides*) is often codominant (Heckscher 2013 p. 99; Faust 2017; Fallon & Heckscher 2021). Deep peat with sphagnum hummocks and dense vegetation appears to be an important habitat feature for this species (C. Heckscher pers. comm. 2022.; Figure 3). Larvae may be restricted to these areas, and adults can be seen emerging from sphagnum hummocks at dusk (NatureServe 2023).

Atlantic white cedar swamps are found in a narrow band along the eastern coastline and Gulf Coast, occurring patchily from Maine to Mississippi (Laderman 1989). On the Delmarva Peninsula, these swamps are found only on the Atlantic Coastal Plain, where they serve as coastal buffer zones and flood control areas, and provide a haven for other rare and imperiled species like Hessel's hairstreak (*Callophrys hesseli*) and the bald cypress sphinx moth (*Isoparce cupressi*). Atlantic white cedar swamps are characterized by slightly elevated hummocks, where the trees grow, surrounded by hollows that are

typically filled with darkly tannic freshwater throughout the growing season (Environmental Protection Agency 2016). Soils are acidic with high levels of organic matter and are characterized by hydrophilic and often rare and unusual plant species (Environmental Protection Agency 2016). Sphagnum mats are common, and can often be found growing over the roots of the cedars (Environmental Protection Agency 2016).



Figure 3. The mysterious lantern firefly is associated with forested peatlands, often characterized by sphagnum mats (left, at the Nanticoke Preserve – Plum Creek Tract in MD) and densely vegetated understories with Atlantic white cedar (right, at Nanticoke Wildlife Area in DE). Photos by Candace Fallon/Xerces Society.

Nanticoke watershed

Five of the six known sites of this species are located in the Nanticoke watershed. Three of these are found within Delaware’s Nanticoke Wildlife Area in tidal freshwater floodplain forests uncommonly co-dominated by Atlantic white cedar (Tiner 2001 p. 6; Heckscher 2013). Further upstream, at The Nature Conservancy’s (TNC) Middleford Preserve, the mysterious lantern firefly can be found in an Atlantic white cedar swamp with red maple, blackgum, loblolly pine, and sweetgum sharing the canopy. In Maryland, the single known site (also a TNC preserve) is located within a forested wetland with a mixed conifer-hardwood canopy of Atlantic white cedar, pine, holly, sweet gum, sassafras, and maple (Firefly Atlas 2022). All five of these sites consist of tidal broadkill mucky peat that is very frequently flooded and sloped Klej-Galloway complex soil (Natural Resources Conservation Services 2022a, 2022b). Very

frequently flooded soils are defined as having a 50% or greater likelihood of flooding in any month of a single year.

Broadkill-Smyrna watershed

The final known site is located within Delaware's Broadkill-Smyrna watershed in a freshwater floodplain peatland forest, characterized by dense shrubs and hardwood forest (Heckscher 2013 p. 99). The most common shrubs in this habitat include sweet pepperbush, blueberry, winterberry, swamp azalea among other species (Tiner 2001 p. 6). This site consists of longmarsh and Indiantown soils that are frequently flooded (Natural Resources Conservation Services 2022c). Frequently flooded soils are defined as soils that have a 50% or greater likelihood of flooding in a single year, while the chances of flooding per month are less than 50%.

Current and potential threats – An assessment of factors

The following factors pose substantial threats to the survival of the mysterious lantern firefly: (1) the present or threatened destruction, modification, or curtailment of its habitat or range, (4) the inadequacy of existing regulatory mechanisms, and (5) other natural or manmade factors affecting its continued existence. Factors 2 (overutilization for commercial, recreational, scientific, or education purposes) and 3 (disease or predation) may also pose potential threats. Below we summarize the rationale and available evidence for all five factors.

1. Present or threatened destruction, modification, or curtailment of habitat or range

Habitat loss and fragmentation

The mysterious lantern firefly is a habitat specialist associated with high quality, low elevation palustrine forested peatland floodplains (Fallon & Heckscher 2021). Once widespread throughout the Delmarva Peninsula, wetland habitats now cover a fraction of the region's landscape. An estimated 40-50% of Delaware's historic wetland habitat has been lost (Tiner 2001), while 45-65% of historic wetlands have been lost in Maryland (Tiner & Burke 1995). From 1982-1991, the greatest loss in wetland habitat in Delaware occurred in palustrine forested floodplains, with an estimated 76% of total wetland loss coming from development in forested floodplains (Tiner 2001 p. 11). From 1992-2007, a further 2,900 acres of palustrine forested floodplains were lost, due to agricultural activities, residential development, highway and road construction, and other types of development (Tiner et al. 2011). As a result of widespread logging and draining to make way for this agriculture and development, Atlantic white cedar—which occurs in palustrine forested floodplain habitats used by the mysterious lantern firefly—is now found in remnant stands that represent a tiny fraction of the tree's historic range (Laderman 1989 p. 18). Fire suppression may also degrade or eliminate Atlantic white cedar habitat by promoting the growth of hardwoods that outcompete this species (Forman & Boerner 1981). As of 2012, there was estimated to be just 4,609.1 acres of Coastal Plain Atlantic White Cedar-Red Maple Swamp, 10.1 acres of Red Maple-Black Gum Swamp, and 61.3 acres of Atlantic White Cedar/Seaside Alder Swamp in all of Delaware (Coxe 2013 p. 101). These swamps are now found mostly in Sussex County, where they occur

along slow-flowing streams and the headwaters of mill ponds (Delaware Division of Fish and Wildlife 2015). They are categorized as a habitat of conservation concern by the state (Delaware Division of Fish and Wildlife 2015).

This history of habitat loss and degradation is especially relevant in the Nanticoke watershed, at the heart of the firefly's range. Prior to European colonization, an estimated 90% of the Nanticoke watershed was palustrine forested wetlands (Tiner 2005). However, land use change, agricultural intensification, and sea level rise have all led to increasing degradation of habitats within the watershed (Tiner 2005). Only a small fraction of remaining Nanticoke wetlands are considered high quality (Tiner et al. 2011), suggesting that the mysterious lantern firefly may have once been much more widespread, but is now limited to a much smaller area due to extensive habitat loss. These fireflies now exist in small, isolated populations separated by poor quality habitat, agricultural fields, and urban development (Figures 2, 4). Fireflies in general are weak fliers and poor dispersers (Lewis 2016 p. 121). If a population were to become extirpated, it is unlikely that individuals from a nearby population would be able to recolonize a site outside of a continuous habitat corridor.

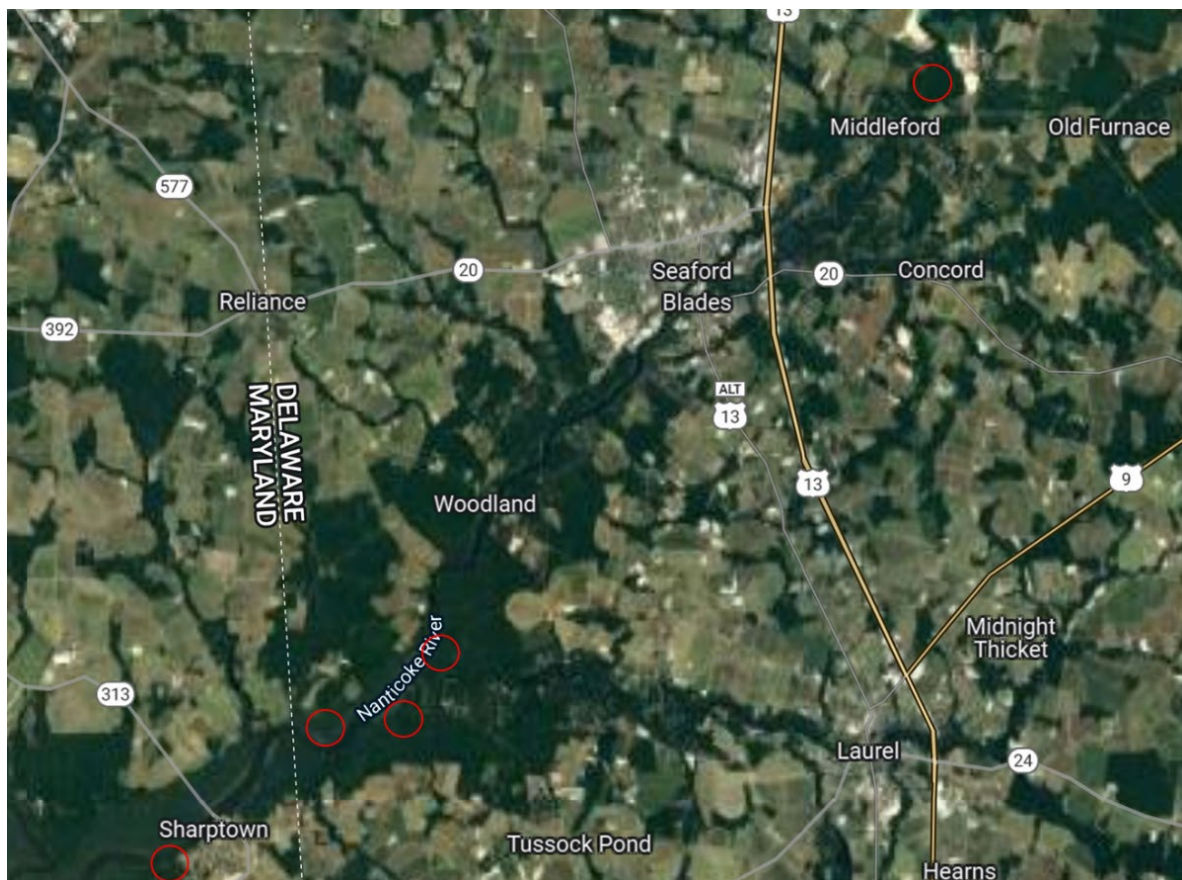


Figure 4. Aerial imagery of the Nanticoke River watershed in Sussex County, Delaware, and Wicomico County, Maryland, relative to mysterious lantern firefly locations (red circles). Dark green indicates natural areas, whereas pale green and cream represent agriculture and urban development. Image from Google Maps.

Invasive species

The mysterious lantern firefly's habitat is characterized by high quality forested peatlands, meaning that invasion by non-native plants will likely have a detrimental effect on this species. In Delaware, 78 species of non-native plants have been identified as known or likely to harm natural habitats, including four that have been categorized as noxious weeds, although these are not the most serious offenders (Delaware Division of Fish and Wildlife 2015). In wetland habitats throughout the state, invasive graminoids pose some of the greatest threats to the mysterious lantern firefly's habitats. One of these, the invasive reed *Phragmites australis australis*, can form dense stands of vegetation that outcompete native species; this plant occupies over 1,000 acres in Sussex County, Delaware alone (Delaware Division of Fish and Wildlife 2015). Another species, Japanese stiltgrass (*Microstegium vimineum*) has been identified as especially problematic for Delaware natural areas. This grass invades the herbaceous layer in cedar swamp habitats used by *P. mysticalampas*, moving outwards from upland areas to surrounding wetlands, where it can become quite dense, completely displacing native species. Japanese stiltgrass has been documented at the mysterious lantern firefly's type locality and has recently (in the last two or three years) begun to invade the floodplain (C. Heckscher pers. comm. 2023).

2. Overutilization for commercial, recreational, scientific, or educational purposes

Prior to the creation of synthetic luciferase in the mid-1990s, fireflies were collected by the millions every year to extract their naturally occurring light producing enzyme, which has many practical uses in biomedical and food safety research (Lewis 2016). From the late 1940s until as recently as the 1980s, harvesting of fireflies was carried out on a large scale across at least 25 states (Lewis 2016 p. 130). By the 1960s, between 500,000 and one million wild fireflies were harvested per year by the public, who were paid by McElroy Labs for their specimens (Lewis 2016). Subsequently, Sigma (now the Sigma-Aldrich Chemical Company) built a network of firefly collectors nationwide that reportedly brought in millions of specimens every year (Lewis 2016).

Firefly harvesters target male fireflies due to males being more visible with more complex light displays than female fireflies (Bauer et al. 2013). Male harvesting can lower female fecundity and survival by removing mate choice, reducing spermatophores available for females to acquire, reducing mating efficiency, and lowering reproductive output (Rooney & Lewis 2002; Lewis et al. 2004; Lewis & Cratsley 2008; South & Lewis 2012; Bauer et al. 2013). These collectors did not discriminate between species, so it is impossible to determine the degree to which *P. mysticalampas* may have been impacted. This species is considered rare; however, it is possible it was more abundant in the past. Although synthetic luciferase has now been available since 1985, and there is no reason for wild harvests to continue, they may still take place at a small scale (Bauer et al. 2013; Lewis 2016). Because of this, overcollection for medical purposes still poses a potential threat to the mysterious lantern firefly.

3. Disease or predation

Many firefly species produce or ingest toxic defense chemicals called lucibufagins to protect themselves from predators, particularly vertebrate predators such as birds (Eisner et al. 1978, 1997). However, despite the presence of these compounds and ability to flash as a warning to predators, fireflies make

up the diet of many animals (Lewis et al. 2012; Faust 2017). Spiders are a well-known predator of fireflies (Lloyd 1973; Long et al. 2012; De Cock et al. 2014), along with other invertebrates including harvestmen and assassin bugs (Lewis et al. 2012; Faust 2017). Adult female mysterious lantern fireflies predate upon other species of firefly (Lewis 2016; Fallon & Heckscher 2021) and may also be predated upon by other fireflies, including closely related and co-occurring species *P. pensylvanica* and *P. lucicrescens* (Faust 2017).

Fireflies are known to suffer from reproductive bacterial parasites (*Wolbachia*, *Spiroplasma*, *Mesoplasma*, and *Entomoplasma*) that can alter sex ratios by causing an increase in female eggs being produced or by killing male eggs (Faust 2017 p. 55). Fireflies can also be afflicted by nematodes that can kill both larvae and adults (Faust 2017 pp. 55–56). Agricultural biocontrol agents can include the use of roundworms to control unwanted pest populations, however this can have the unintended consequence of killing fireflies (Faust 2017). Various fungi, mites, and multiple species of parasitic fly also threaten firefly health (Faust 2017).

While it is unknown if the mysterious lantern firefly is threatened by disease, it is known to co-occur with predatory firefly species, and for species like this that are already experiencing declines within highly localized ranges, natural predation and disease rates can compound existing threats.

4. Inadequacy of existing regulatory mechanisms

The mysterious lantern firefly has been recorded on federal (Prime Hook National Wildlife Refuge), state (Nanticoke Wildlife Area), and private (The Nature Conservancy's Nanticoke and Middleford North Preserves) lands. While some level of passive protection comes from existing on conservation lands, this firefly is not protected from many of the threats it faces, including sea level rise from climate change (Delaware Coastal Programs 2012). Furthermore, no existing regulatory mechanisms adequately protect the mysterious lantern firefly at the federal, state, or local level. Accordingly, the lack of effective regulatory mechanisms for mysterious lantern fireflies, in concert with the species' limited range and historic and ongoing decline in quality and availability of habitat, underscores the critical need to provide this firefly with protection under the Endangered Species Act. Receiving listing under the ESA would protect the mysterious lantern firefly and its critical habitat by instilling protective restrictions on management activities and other actions that could degrade or eliminate habitat.

Federal regulatory mechanisms

There are no existing federal regulatory mechanisms with the specific intent to ensure the mysterious lantern firefly's long-term survival and recovery, although some federal wetland laws may be applicable to the Atlantic white cedar wetland habitat this species utilizes. For example, Section 404 of the Clean Water Act of 1977 prohibits the discharge of dredge or fill material into "navigable waters" without an Army Corps of Engineers permit. However, the Corps defines navigable waters as "those waters subject to the ebb and flow of the tide shoreward to the mean high water mark and/or are presently used, or have been used in the past, or may be susceptible for use to transport interstate or foreign commerce,"

which is unlikely to include the types of wetland habitats where *P. mysticalampas* is found, meaning the prohibition does not apply.

This species is threatened by pesticide use across its range. The U.S. Environmental Protection Agency (EPA) licenses the sale and use of the insecticides that threaten the mysterious lantern firefly. These pesticides are regulated under the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA), which directs EPA to register a pesticide only once it has been deemed that its appropriate use will not cause unreasonable harm to the environment. Unfortunately, EPA has yet to consider the broad suite of population-level impacts that pesticides can have on fireflies, and despite the fact that the EPA is now considering impacts of approved pesticides on listed insects, there are currently no listed fireflies whose considerations could apply to this species. Furthermore, pesticides are not tested directly on fireflies or other beetles, but rather on surrogate invertebrate species such as the western honeybee (*Apis mellifera*), water fleas (*Daphnia*), and scud (*Gammarus fasciatus*). None of these three invertebrate species inhabit the soil for any part of their life cycle, nor are they beetles, so they are likely inadequate surrogates for fireflies. The EPA also does not require that the additive or synergistic effects of insecticides, herbicides, or fungicides be considered, even though pesticides are normally found in combination, not singly.

In addition to the lack of broad federal regulatory mechanisms that might protect this species, no specific protective regulatory mechanisms for mysterious lantern fireflies are in place on federal lands where the species occurs. Prime Hook National Wildlife Refuge, the only known federal site to host this species, was established in 1963 as a sanctuary for migratory birds in the Atlantic Flyway (United States Fish and Wildlife Service 2022). By 2007, the refuge had expanded to over 10,000 acres and now belongs to the Coastal Delaware National Wildlife Refuge Complex (United States Fish and Wildlife Service 2022). Using funding from Hurricane Sandy Disaster Relief Act, the refuge recently completed one of the largest coastal wetland habitat restoration projects (~4,000 acres) in the eastern United States (United States Fish and Wildlife Service 2022). The restoration project improves the refuge's ability to withstand future storms and sea level rise, which could benefit the mysterious lantern firefly. Although promising, these efforts cannot be considered adequate regulatory mechanisms to protect and recover the mysterious lantern firefly, since this affects only one disjunct site where the species occurs. The mysterious lantern firefly is also not listed as a species of priority or concern within the refuge (Latterell 2009), suggesting its specific life history and habitat needs were not taken into consideration during restoration efforts.

Species such as the mysterious lantern firefly can sometimes benefit from critical habitat designations for other species listed under the Endangered Species Act. However, to our knowledge, no critical habitat designations overlap with any known *Photuris mysticalampas* localities, so these designations do not protect *P. mysticalampas* from decline and extinction.

State regulatory mechanisms

To the best of the petitioners' knowledge, there are also no existing regulatory mechanisms at the state level that are adequate to protect the mysterious lantern firefly in Delaware or Maryland. While permits

are required by the Delaware Division of Fish and Wildlife to collect protected wildlife, finfish, shellfish or their nests or eggs for scientific, education, or propagating purposes (Delaware Department of Natural Resources and Environmental Control 2022a), the mysterious lantern firefly is not protected under the state endangered species act, so this regulation does not appear to apply. In Maryland, wildlife collection permits are required for “birds, nests or eggs, mammals, reptiles, amphibians” (Maryland OneStop 2023) and do not appear to be needed for unprotected insects like the mysterious lantern firefly.

Activities in tidal and nontidal wetlands are regulated through Maryland’s Tidal Wetlands and Nontidal Wetlands Acts and Delaware’s Wetlands Act and Subaqueous Lands Act. However, in both states, permits may be obtained for projects including dredging, draining, filling, construction, bulkheading, mining, drilling, and excavation. Furthermore, isolated wetlands are not protected. Consequently, none of these acts appear to offer the mysterious lantern firefly protection against extinction.

Delaware’s Chapter 7 Title 71.A Regulation of Outdoor Lighting dictates that “an outdoor lighting fixture may be designed, installed or replaced using state funds only if” certain standards are met (State of Delaware 2023). However, these regulations only apply to state-funded outdoor lighting, and provide a number of exemptions for safety, emergency use, and special events.

While no populations are yet known from state-managed sites in Maryland, three of the six known sites for this species occur within Delaware’s Nanticoke Wildlife Area, a state wildlife area encompassing three large land tracts over 4,510 acres (Delaware Department of Natural Resources and Environmental Control 2022b). Habitat management focuses on wetland restoration and reduction in water pollution throughout the Nanticoke watershed (Delaware Department of Natural Resources and Environmental Control 2022c), which could indirectly benefit this firefly and its habitat, but is not substantive enough to ensure its persistence. Furthermore, although the mysterious lantern firefly is recognized as a Species of Greatest Conservation Need (SGCN) in Delaware’s State Wildlife Action Plan (Delaware Division of Fish and Wildlife 2015), this again does not offer any regulatory protection. Although Maryland also includes fireflies as SGCN (Maryland Department of Natural Resources 2015), this species is not listed, as it was not known to occur in the state until 2022.

Local regulatory mechanisms

There are no known county or city-level regulatory mechanisms that would protect the mysterious lantern firefly in Delaware or Maryland. Sussex County, DE, and Wicomico County, MD, have some outdoor lighting standards as part of their zoning and development standards, which are aimed at minimizing light pollution in the form of glare, light trespass, and sky glow. However, in some cases these codes and standards require outdoor lighting for safety reasons or provide exemptions for sources of light pollution for safety reasons and do not adequately curtail light pollution and its impacts on fireflies. Existing lighting codes and ordinances do not have the explicit goal of protecting *Photuris mysticalampas* or other nocturnal insects from harmful artificial light at night, and so are insufficient in protecting this firefly from light pollution.

Private lands

Two known mysterious lantern firefly sites occur on private conservation lands owned and managed as preserves by the Nature Conservancy. One of these sites, Middleford North Preserve, is a small undisturbed tract along the Nanticoke River that provides a haven to multiple imperiled plants, butterflies, and fish species. The second site is located within the Nanticoke Preserve, a 50-mile corridor of protected habitat along the western shoreline of the Nanticoke River that was established through a coalition of public and private partners in Maryland and Delaware (The Nature Conservancy 2022). The Plum Creek Tract, a ~25.9 acre parcel within this corridor where *P. mysticalampas* was discovered in 2022, has a history of clear-cutting and prescribed fire (Wilson 2007, 2009). Recent management efforts at this site appear to be focused on assisted migration of longleaf pine—site managers are planting this species north of its historic range as an experiment to determine whether human intervention can help it persist as the climate warms (Lumpkin 2020; Popkin 2022). Regular burning to mimic the natural fire regimes that these trees require is a fundamental part of this effort. It is unclear what impact these actions have on the mysterious lantern firefly and its habitat (fire suppression being one potential threat to this species' Atlantic white cedar habitat, as it promotes the growth of competing hardwoods; (Forman & Boerner 1981), but regardless of their effect, they do not constitute regulatory mechanisms that protect the species.

5. Other natural or manmade factors affecting this firefly's continued existence

Further factors threaten the mysterious firefly's continued existence including climate change, light pollution, pesticide use, and declines in the species' primary food source, as described in detail below.

Climate change

Annual temperatures in North America have increased at an average rate of 0.13°C (0.23°F) since 1910 (National Oceanic and Atmospheric Administration 2022). As global climate change occurs, temperatures are expected to continue to increase, resulting in increased sea level rise, increased frequency of severe weather events, and further habitat degradation or loss of ecosystems.

Sea level rise

On the East Coast of the United States, sea levels are predicted to rise 10-14 inches by 2050 (National Oceanic and Atmospheric Administration 2022). Delaware is especially at risk of sea level rise, due to low-lying ground and structures throughout the state (Delaware Coastal Programs 2012). The rate of sea level rise in Delaware is estimated to be twice the global average, increasing an average of 0.13 inches every year (Delaware Coastal Programs 2012); by 2100, sea levels in the state are expected to increase 2-6ft (Delaware Division of Fish and Wildlife 2015). Sea levels for Sussex County, where the majority of known *P. mysticalampas* populations occur, are predicted to rise two feet even sooner, between 2053 (high projection) and 2073 (intermediate low projection) (National Oceanic and Atmospheric Administration 2022). As such, all low lying areas including the floodplain habitats where the mysterious lantern firefly occurs are at a high risk of flooding within the next 50 years (Delaware Division of Fish and Wildlife 2015). While these floodplain systems are built to withstand certain amounts of flooding, increases of this nature could inundate the Atlantic white cedar swamp habitats where the firefly

occurs, effectively submerging and killing cedar trees that occur in slightly elevated hummocks, and altering the habitat in such a way that it may no longer be suitable for the firefly. This type of scenario is not limited to the mysterious lantern firefly; the State of Delaware lists rising sea levels as a primary threat to Species of Greatest Conservation Need (a designation shared by the mysterious lantern firefly) in its State Wildlife Action Plan (Delaware Division of Fish and Wildlife 2015).

While the sites located within the Nanticoke River watershed are further inland, they are still tidally influenced and susceptible to sea level rise. However, the single known site along the Atlantic coast may be particularly at risk of this threat due to its proximity to the ocean. It is predicted that by 2050 half of the upland area within Prime Hook NWR, one of the areas where the mysterious lantern firefly occurs, will be converted to wetlands or open water with the worst case scenario predicting only 1% of upland habitat remaining (Delaware Division of Fish and Wildlife 2015 p. 45). Furthermore, since mysterious lantern fireflies require freshwater habitats, sites with coastal influence are at high risk of saltwater inundation due to sea level rise and storm surges. For example, dune breaches at Prime Hook NWR during Hurricane Sandy caused significant saltwater intrusion in the refuge's freshwater marshes; although some freshwater and brackish areas remain, most has been converted to saltwater (American Littoral Society 2012). This type of saltwater inundation can degrade or eliminate the habitat that mysterious lantern firefly eggs and larvae are dependent on.

Increased temperatures and phenology changes

Annual temperatures in Delaware are expected to increase between 1.5-2.5°F from 2020-2039, and 2.5-4.5°F between 2040-2059 (Delaware Division of Fish and Wildlife 2015). Temperature increases are expected to disproportionately affect spring and summer months compared to fall and winter (Delaware Division of Fish and Wildlife 2015). This can negatively affect the mysterious lantern firefly's survival because temperatures influence breeding and egg and larval success during development, as well as habitat suitability (Bauer et al. 2013; Evans et al. 2019). Additionally, any increased incidence of drought due to persistent heat will also exacerbate declining firefly populations due to threat of desiccation (Evans et al. 2019).

Degree days are a measure of accumulation of heat over the course of a growing season, used to describe and predict the activity and development of organisms in temperate regions. Degree days can be used to predict timing of male emergence, female emergence, and peak display (Faust 2017). As fireflies respond to degree days, increasing temperatures can alter firefly phenology by advancing the dates of male, female, and/or peak emergence/display time (Faust & Weston 2009; Faust 2017). Already the synchronous firefly, *Photinus carolinus*, now has a peak display 10 days earlier than 20 years ago (Lewis 2016). Firefly eggs and larvae are also susceptible to changing environmental conditions, desiccating in too dry microhabitats or molding in too humid of conditions (Evans et al. 2019). Additionally, firefly larvae take years to develop and a stochastic environmental change such as a single flood or weather event can therefore affect a population of fireflies and larvae for years (Faust 2017).

Altered precipitation regimes and increased incidence of severe weather

The current predicted warming models estimate a higher incidence of storm events in eastern North America. Delaware is projected to have more intense and frequent flooding, hotter and dryer days, and more intense precipitation events (Delaware Division of Fish and Wildlife 2015). Changes in frequency of severe weather incidence have predicted increased mortality for Delaware's native flora and fauna due to floods, drought, and heat (Delaware Division of Fish and Wildlife 2015). As sea levels rise, storm surges are expected to become more intense, increasing chances of flooding (Delaware Division of Fish and Wildlife 2015). Additionally, storm surges can cause salt water inundation at levels higher than those recorded in the past due to sea level rise (Delaware Division of Fish and Wildlife 2015). The mysterious lantern firefly has been recorded in the Nanticoke Wildlife Area along the Nanticoke River floodplain. Due to the proximity to the river, the mysterious lantern firefly is especially at risk of extreme flooding events in this location.

Light pollution

Many firefly species are dependent on bioluminescent courtship patterns to locate mates and do not use other visual or chemical cues (Lloyd 1966; Stanger-Hall & Lloyd 2015; Owens & Lewis 2022). Flashing fireflies are thus sensitive to light and use ambient darkness as a cue to time their flashing behavior (Lewis 2016). Light pollution from urbanization and infrastructure is therefore a serious threat to fireflies, in particular those that display at night rather than at dusk (Owens & Lewis 2018, 2022). Mysterious lantern fireflies fall into this category, flashing only in total darkness (Heckscher 2013 p. 93), and are therefore likely very sensitive to light pollution.

Artificial light can change the timing of firefly flashes in addition to intensity and frequency of flashes (Owens & Lewis 2018). Flashing fireflies are lower in abundance and activity in urban areas (Picchi et al. 2013; Hagen et al. 2015; Owens & Lewis 2022) and in areas near artificial lights (Owens & Lewis 2022). Females are especially adversely impacted by artificial lights, with females under artificial lights non-responsive to nearby males (Owens & Lewis 2021, 2022). Some males may readily come to light of any kind including artificial light (Firebaugh & Haynes 2019; Owens & Lewis 2022), while for other species males are repelled by artificial light (Faust 2017; Branham & Faust 2019; Owens & Lewis 2022).

Artificial light at night may reduce the reproductive success of the mysterious lantern firefly since this species is only active in complete darkness. Without courtship flashing the males and females will be unable to detect one another. While most known mysterious lantern firefly sites show relatively low levels of radiance, high levels of light pollution in developed areas along Routes 13, 113, and 1 fragment and encroach upon the firefly's habitat (Figure 5). Therefore regulations on outdoor lighting and limits on urbanization within designated critical habitat are necessary to protect the mysterious lantern firefly.

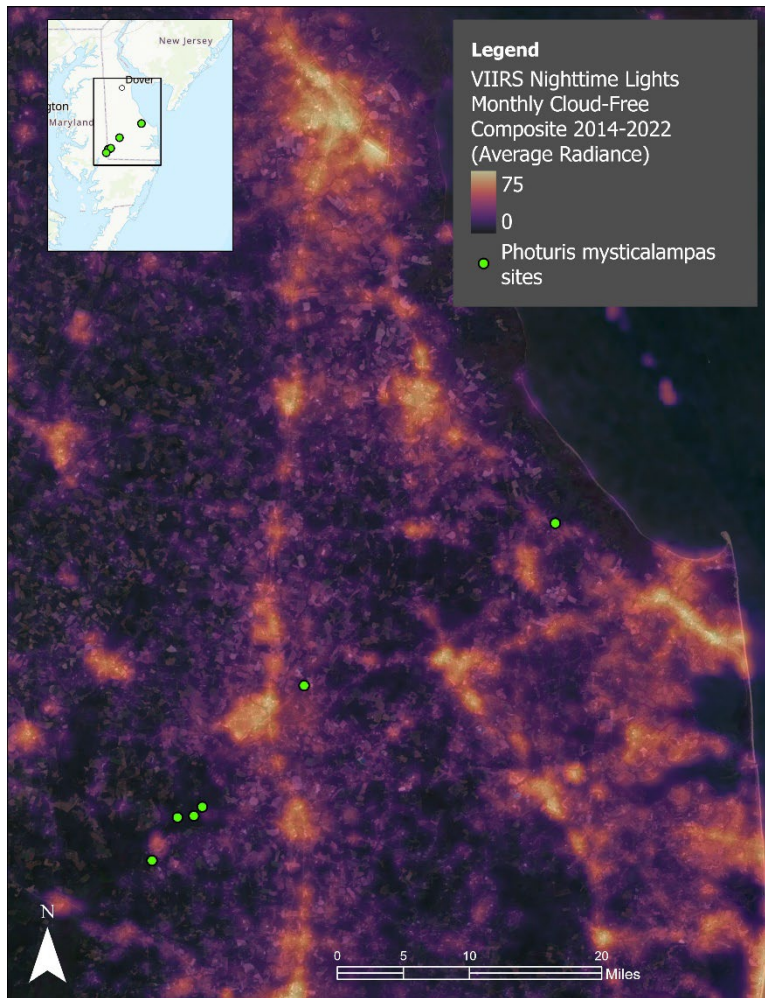


Figure 5. Light pollution in the vicinity of known mysterious lantern firefly localities (green dots) on the Delmarva Peninsula of Maryland and Delaware. Colors represent amounts of artificial light at night, ranging from black (low amounts of artificial light) to yellow (high amounts of artificial light). Light is measured in average of radiance (10^{-9} Watts/cm²/sr) during the period of 2014-2022. While remote-sensed radiance at this scale is an imperfect proxy for biologically relevant artificial light at the ground level, the two are correlated. Radiance imagery from the Earth Observation Group, Payne Institute for Public Policy.

Pesticides and other pollutants

Pesticides are identified as a serious threat to firefly conservation in North America, second only to habitat loss and fragmentation, according to a survey of firefly experts (Lewis et al. 2020). Drift, runoff, or groundwater movement of pesticides from adjacent agricultural and urban landscapes are the most likely ways in which contaminants enter *P. mysticalampas* habitat; however, woodland habitats where this species occur may also be treated with pesticides directly. Fireflies may absorb pesticide through direct contact with airborne pesticides, or through contact with contaminated surfaces, sediments, surface water, and/or groundwater. Given that *P. mysticalampas* inhabits floodplain forests, residues of agricultural pesticides in surface water and sediment carried by floodwaters that may periodically settle over their habitat can pose a direct route of exposure. Larvae, which spend approximately two years in

soil, may experience chronic contact and oral exposure to soils that contain pesticides, especially those pesticides that are persistent in soil such as the neonicotinoids. Consumption of contaminated prey and contact with contaminated vegetation are other potential routes of exposure.

Of all pesticides, insecticides are the type most likely to harm fireflies as many are “broad-spectrum” (i.e. toxic to a wide variety of insects) and some are designed to target pests within the beetle order Coleoptera. Pesticide uses in terrestrial sites (such as agricultural and urban areas) pose a significant threat to the mysterious lantern firefly because these pesticides are regularly transported via runoff into streams and rivers, as well as into groundwater. These polluted waters, which regularly flood *P. mysticalampas* habitat, likely result in chronic exposure to *P. mysticalampas* individuals and their prey.

Within the counties where *P. mysticalampas* has been documented to occur, land use is largely divided between farmland and natural areas. In Sussex County, DE, farmland comprises 36% of the landcover; within the Nanticoke watershed more broadly (which encompasses the one known site in Maryland), it comprises 45% of the land cover (Nanticoke Watershed Alliance n.d.). Within these farmlands, poultry (supported by corn), wheat, and soybean crops for feed are the largest agricultural uses. Specialty crops such as vegetables, grapes, and grass-fed dairy also occur in the area. Developed land varies across the current range of *P. mysticalampas*, but is relatively low (8% in the Nanticoke watershed according to the (Nanticoke Watershed Alliance n.d.).

Mosquito control administered by the Delaware Department of Natural Resources and Environmental Control (DDNREC) is another chronic source of pesticide exposure that poses a serious risk to *P. mysticalampas*. Delaware has been characterized as possessing “world-class mosquito-producing habitat” (Lauria 2022). The state conducts mosquito control from March through early November each year, utilizing helicopters, planes, and ground-based truck foggers to spread insecticides targeted at either larval or adult mosquitoes, depending upon the season.

Pesticides used within the region for agricultural, urban, or forestry purposes and for mosquito control make their way into habitats that may contain *P. mysticalampas*, threatening the species with increased mortality and harmful sub-lethal effects, as well as harmful effects on prey species such as worms and snails.

Given local land uses and mosquito spray efforts, pyrethroids, neonicotinoids, organophosphates, and some mosquito larvicides are likely the most significant direct pesticide threats to *P. mysticalampas*. Documented effects of some of these compounds on fireflies, beetles, and other non-target invertebrates, as well as information about the uses and routes of exposure of these chemicals are laid out in the following sections.

Pyrethroids: Nationwide, in both surface waters and sediments, pyrethroids are the class of insecticides most likely to occur at concentrations higher than regulatory thresholds (Wolfram et al. 2018). However, these pesticides may be missed by sampling programs that focus exclusively on water sampling, since pyrethroids partition into sediments. Pyrethroids have a wide range of uses in agricultural, urban, and

non-crop (such as mosquito management) arenas. For example, corn, soybean, and wheat crops (which make up the majority of farmland uses within the range of the mysterious lantern firefly) are grown with an intensive mix of agricultural chemicals, including pyrethroids—some applied as sprays to the growing crop and others applied directly to the seed or soil. Pyrethroids are applied foliarly to 62% of planted corn acres nationwide, 65% of soybean acres, and 62% of wheat acres—all crops that are grown within the range of the mysterious lantern firefly. Twenty-seven percent of corn acres also receive soil applications of pyrethroids (Michell 2017).

Nowak et al. (2017) reported that beetles (as a group) comprise the second most targeted pest by agricultural pyrethroid users, indicating the efficacy of pyrethroids on Coleoptera in general. Peterson et al. (2016) observed high mortality for adult lady beetles contacted by ground-based ULV mosquito spraying with permethrin (a pyrethroid closely related to sumithrin and sometimes used in Delaware). Beachley (2008) assessed pyrethroid mosquito abatement ULV sprays on non-target insects and found that survival rates for exposed lady beetles (*Hippodamia convergens*) placed 25 m from the spray were significantly lower 1, 12, and 24 hours post-spraying compared to non-exposed controls. Tefluthrin, a pyrethroid used to control wireworms, reduced the density of beetles in a field study where it was applied (Babendreier et al. 2015). These studies suggest that pyrethroids may have lethal effects on other beetle species, such as fireflies.

Pyrethroids are generally the insecticide of choice when doing ground-level spraying for adult mosquito control, used both by vector control districts and by pest control companies treating individual properties. In Delaware and Maryland, residential mosquito sprays likely comprise a significant percentage of home pesticide treatments. The vegetated perimeters of residential properties are often sprayed by homeowners and/or pest control companies, killing mosquitoes that rest in or later contact the vegetation. Home mosquito sprays, typically with pyrethroids, generate about 20% of pest control company revenues, according to trade data (Flesher 2022). Numerous pest control companies offer residential mosquito control pesticide treatments in the counties where the mysterious lantern firefly occurs.

At the state level, the DDNREC focuses early season efforts on the control of larval mosquitoes, but when larvicides are unsuccessful the Department uses adulticides, including synthetic pyrethroids such as sumithrin, deltamethrin, etofenprox, or organophosphates such as naled. Adulticides are preferably applied adjacent to aquatic mosquito breeding sites just after emergence. However, the window for this targeted approach is short, and more extensive areas may be treated.

Delaware divides the state into a grid pattern to schedule and announce mosquito treatment areas. Each grid cell encompasses approximately 12 square miles (Delaware Department of Natural Resources and Environmental Control 2022d). Publicly available announcements do not disclose exactly where treatments take place within each grid cell. The areas currently inhabited by *P. mysticalampas* are located within or adjacent to grid cells 170, 180, 182 (Broad Creek) and 129 (Prime Hook NWR). During 2022, areas within these grid cells were scheduled for treatment on multiple dates (Delaware

Department of Natural Resources and Environmental Control 2022e; Table 3). These state records show the repeated, systematic use of adulticide mosquito sprays over widespread areas of Delaware—which may expose adult fireflies, especially given that adulticide sprays occur during evening/night hours when adults are active. In contrast, Maryland does not provide easily publicly accessible records of state-administered mosquito treatments, and so the extent of application in that state where the mysterious lantern firefly occurs is unclear.

Table 3. Mosquito treatment applications by date, chemical and time, in 2022, near or within *P. mysticalampas* habitat (Grids 170, 180, 182, and 129 are all within or near the firefly’s habitat) (Delaware Department of Natural Resources and Environmental Control 2022e). Records are also available for prior years.

Date	Grid(s)	Active Ingredient	Pesticide Group	Method	Time
<i>March/April</i>					
None					
<i>May</i>					
24 th	170, 182	Sumithrin/PBO	Pyrethroid	truck	evening/night
<i>June</i>					
1 st	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
7 th	182	Sumithrin/PBO	Pyrethroid	truck	evening/night
9 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
23 rd	182	Sumithrin/PBO	Pyrethroid	truck	evening/night
27 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
28 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
30 th	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
<i>July</i>					
7 th	129	Naled	Organophosphate	airplane	evening
11 th	129	Methoprene	Larvicide insect, Growth regulator	airplane	evening/night
14 th	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
18 th	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
21 st	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
26 th	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
27 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
<i>August</i>					
2 nd	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
3 rd	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
8 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
9 th	170	Sumithrin/PBO	Pyrethroid	truck	evening/night
16 th	182	Sumithrin/PBO	Pyrethroid	truck	evening/night
17 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night

Date	Grid(s)	Active Ingredient	Pesticide Group	Method	Time
23 rd	182	Sumithrin/PBO	Pyrethroid	truck	evening/night
24 th	129	Sumithrin/PBO	Pyrethroid	truck	evening/night
29 th	129	Naled	Organophosphate	airplane	evening
September					
6 th	170,182	Sumithrin/PBO	Pyrethroid	truck	evening/night
21 st	129	Naled	Organophosphate	airplane	evening
27 th	129	Naled	Organophosphate	airplane	evening
28 th	129	Naled	Organophosphate	airplane	evening

Mosquito adulticides are intended to remain suspended in air for some time to target flying adults, hence the use of Ultra Low Volume (ULV) technology for adulticides (and some larvicides), which results in very fine droplets being dispersed into the air. Both ground and aerial applications of insecticides using ULV technology can result in substantial drift of the insecticide. Schleier and Peterson (2010) performed field studies to measure environmental concentrations of ground-based ULV-applied insecticides in flat grassland sites. The authors observed that an average of 10.4% of the insecticides sprayed settled out within 180 m (591 ft.) of the spray source, meaning that the rest dispersed further. According to the authors, these results are similar to measurements in other studies of ground-based ULV applications using both pyrethroid and organophosphate insecticides, which found 1 to 30% of the insecticide sprayed deposits on the ground within 100 m (328 ft.) of the spray source. Sumithrin (also known as d-phenothrin) is a pyrethroid chemical; the product utilized by DDNREC is formulated with piperonyl butoxide (or PBO), a synergist which increases the effectiveness of phenothrin. Sumithrin breaks down relatively rapidly in upland soils but is far more persistent in flooded soils (Jackson et al. 2011), meaning that the forested floodplains inhabited by *P. mysticalampas* may contain chronic residues of this mosquito insecticide. Like other pyrethroids, sumithrin binds to suspended solids and bottom sediment in water.

Since pyrethroids effectively kill other types of beetles, they are likely effective at killing fireflies. Because they are used within the range of the mysterious lantern firefly for landscaping, agricultural, and mosquito control purposes, pyrethroids pose a significant threat to the mysterious lantern firefly.

Neonicotinoids: Neonicotinoids are the most widely used class of insecticides in the world. Because of their widespread use in agriculture and urban landscapes, and their water solubility, they are routinely found in runoff. For example, the U.S. Geological Survey has frequently detected neonicotinoids in streams across the Midwest in areas where corn and soybean are grown (Hladik et al. 2014). Sediment samples taken in floodplain wetlands throughout Missouri consistently found neonicotinoids (>60% of samples) in all sampling periods, driven by the local extent of agriculture and treated seed planting (Kuechle et al. 2019). Given the high percentage of agricultural lands found within the watersheds where *P. mysticalampas* is known to occur, it is likely that neonicotinoids are present in runoff here as well.

Groundwater can also be contaminated by pesticides. Groundwater samples from corn and soybean growing areas in the Midwest, where seed treatments had occurred for six growing seasons (and ceased for one growing season prior to the study) contained the neonicotinoid clothianidin, with mean concentrations of 72, 41, and 30 ng/L in three sampling periods (Hladik et al. 2017). Other studies have found higher concentrations of clothianidin in groundwater; mean groundwater concentrations exceeding 120 ng/L were reported by De Perre et al. (2015). Streams and rivers draining developed areas are not immune from these pollutants. In fact, pesticides and particularly insecticides are routinely found in urban waterways at concentrations harmful to aquatic life (Stone et al. 2014; Stehle et al. 2019). Urban pesticide uses are known to result in significant water pollution, due to the higher pesticide concentrations often allowed in urban environments, coupled with the substantial runoff associated with lawns and developed environments. For example, turf applications of neonicotinoids resulted in soil concentrations three times higher than those typical in row crops (Armbrust & Peeler 2002). Soil drenches of neonicotinoids, which are common in towns and cities for managing pests on trees, shrubs and other ornamentals, resulted in concentrations of neonicotinoids 8-40x higher than typical agricultural soil neonicotinoid concentrations (Knoepp et al. 2012; Schaafsma et al. 2016; Radolinski et al. 2019; Pearsons et al. 2021b).

Neonicotinoid insecticides used and/or detected in the environment in Delaware and Maryland include clothianidin and, to a lesser degree, imidacloprid (Figures 6 and 7). An estimated 90% of corn, 76% of soybean and 56% of winter wheat acres in the United States are planted with seed that are coated with pesticides (Crop Life Foundation 2013; Kynetec 2019; Hitaj et al. 2020). Neonicotinoid insecticides (clothianidin, thiamethoxam and/or imidacloprid) are the most common seed coatings on corn, typically in combination with one or more fungicides, including captan, carboxin, metalaxyl, and triticonazole. The mix of pesticides available for soybeans and wheat seed treatments are similar to that used in corn (Crop Life Foundation 2013). Imidacloprid is commonly applied in corn, soybean, and other row crops as a foliar insecticide or applied as a coating on seeds. Large-scale planting of treated seeds can result in contamination of soils, waterways, and nontarget plants in row crop landscapes (Bonmatin et al. 2015). Imidacloprid is also used in tree farms, forestry, and urban sites.

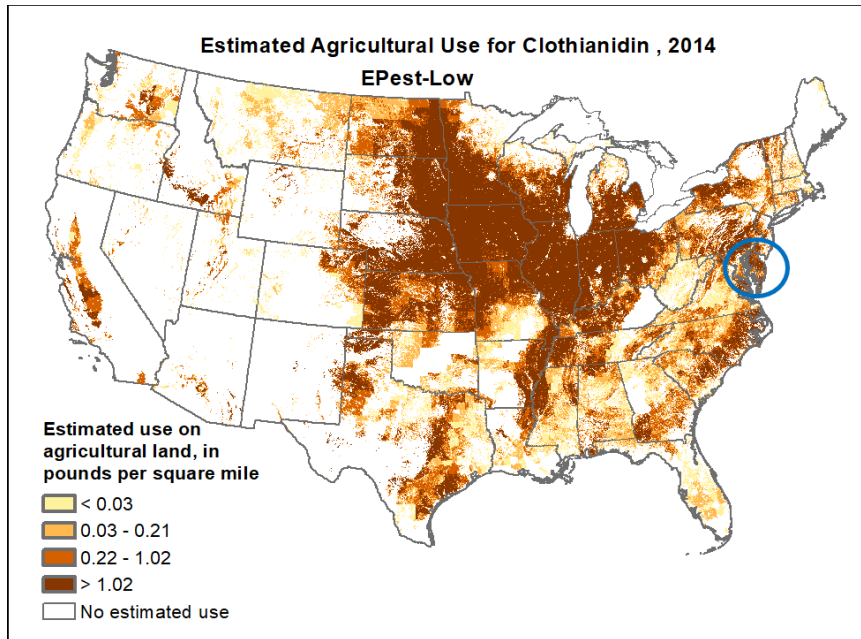


Figure 6. Lower-bound estimated agricultural application rates of the neonicotinoid clothianidin in the year 2014. Estimates from after 2014 do not include seed treatments, which is one of the primary uses of the compound. Note that clothianidin was applied on the Delmarva Peninsula, where *Photuris mysticalampas* is known to occur (blue circle). Map from U.S. Geological Survey Pesticide National Synthesis Project.

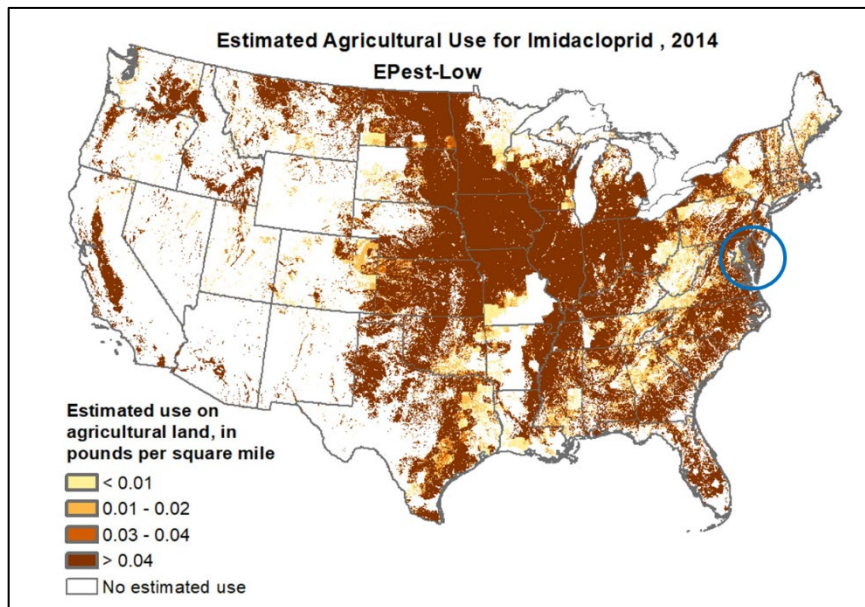


Figure 7. Preliminary lower-bound estimated agricultural application rates of the neonicotinoid imidacloprid in the year 2014. Note that imidacloprid is heavily used within the range of *Photuris mysticalampas* on the Delmarva Peninsula (blue circle). Estimates from after 2014 do not include seed treatments, which is a significant use of the compound; hence, we show data from 2014. Map from U.S. Geological Survey Pesticide National Synthesis Project.

Forested habitats in Delaware contain ash trees (although they are a minor component) and ash are a common street tree in towns and cities. Within the Nanticoke Preserve's corridor where *P. mysticalampas* occurs, a major focus is on the conservation of ash trees. These trees, while able to tolerate tidal flooding common in the corridor, are threatened by the invasive emerald ash-borer beetle, *Agrilus planipennis* (The Nature Conservancy 2022). Clusters of ash trees within the preserve are treated proactively with pesticides to help slow and prevent the spread of this beetle, which kills most ash trees and was detected in Sussex County in 2018. The insecticides recommended for control of this coleopteran pest (generally emamectin benzoate or imidacloprid) make their way to leaf tissue. As leaves fall, the residual insecticide in the leaves may be introduced to soil or directly into water. Kreuzweiser et al. (2007) measured imidacloprid residues in leaves from treated trees at 800-1300 ng/g, and found that the higher residue levels significantly inhibited feeding of leaf-shredding insects. Treatment of emerald ash borers may threaten the mysterious lantern firefly because the compounds used are effective at killing beetles generally. In addition, the areas treated may overlap with the areas where the mysterious lantern firefly occurs.

Soils contaminated with neonicotinoids have been shown to have negative impacts on fireflies and/or other beetles. Disque et al. (2019) captured seventy percent fewer adult fireflies in plots planted with corn seed coated with the neonicotinoid clothianidin, compared to untreated plots, an effect attributed to impacts on firefly larvae. A laboratory study on the effects of clothianidin on the North American fireflies *Photinus pyralis* and *Photuris versicolor* found sublethal behavioral effects, including reduced feeding and soil-chamber building (Pearsons et al. 2021a). At concentrations above 1,000 ng/g (equivalent to 1000 ppb, higher than those found in most agricultural soils), larvae also exhibited long-term immobility and mortality.

Wang et al. (2022) studied the effects of imidacloprid applied topically to larval *Pyrocoelia analis* fireflies at concentrations of 0.025-0.4 mg/L (approximately 25-400 ppb, within the range of concentrations commonly seen in field residue studies) and found destructive changes in midgut and fat cell tissues, persistent luminescence. The authors also determined an LC₁₀ level of 0.1 mg/L.

Laboratory experiments conducted on an Asian firefly species, *Aquatica lateralis*, showed that, at recommended concentration, the neonic thiamethoxam caused more than 80% mortality to both adults and larvae and significantly reduced egg hatching (Lee et al. 2008). (Note that the 2008 label for the product used in the Korean could not be located by Xerces staff and it is possible that the recommended label rate was higher than what is authorized currently in the U.S.) Carabid beetle species exposed to corn seedlings coated with field-relevant rates of imidacloprid, thiamethoxam and/or clothianidin had nearly 100% mortality (Mullin et al. 2005). Several beetle species also showed sublethal effects from contact with soil treated with imidacloprid (Pisa et al. 2015). Application of imidacloprid to a lawn to target white grubs (the larvae of various beetle species) was found to reduce non-target species including beetles by 50% or more over three years (Peck 2009).

Larval fireflies may also be exposed to neonicotinoids through their prey, which include gastropods such as slugs. Slugs are relatively insensitive to some insecticides, but residues in slug bodies can be transmitted to their predators. Researchers examining predaceous slug-consuming beetles found that slugs were unaffected by thiamethoxam but transmitted the insecticide to the beetles feeding on them, impairing or killing more than 60% of the beetles (Douglas et al. 2015). Similar pathways could occur with snails, which have been shown to become contaminated with certain pesticides (Druart et al. 2011). Developing fireflies may thus be negatively impacted by pesticide use that can contaminate their food sources.

These studies show that the mysterious lantern firefly is threatened by direct mortality and sub-lethal negative effects from exposure to neonicotinoids used within agricultural areas and towns and cities adjacent to and upstream of *P. mysticalampas* habitat. These insecticides are widespread both in their level of application and their presence in wetlands. They pose a significant threat to *P. mysticalampas* due to both persistence in the environment and their toxicity to fireflies.

Organophosphates: Organophosphates, a group of highly toxic, broad-spectrum insecticides, are used in agriculture and mosquito control. Several organophosphates have been shown to kill fireflies at use rates recommended by the manufacturer on the label, including acephate, fenthion and diazinon (Lee et al. 2008).

Other organophosphates that are broadly toxic to insects and used for adult mosquito control by vector districts include malathion and naled. Both of these chemicals may be sprayed as aerosols by aerial means, or by ground-based truck “foggers,” resulting in substantial drift. For example, naled drift was measured as far as 750 m from an application site in a study in Florida (Hennessey et al. 1992). Naled, which is used for mosquito control in Delaware, may be present in the air for many days after a spray, exposing fireflies and other flying insects; according to the EPA, naled’s half-life in air is 57.8 hours, meaning detectable levels could last for approximately 10 days after a spray. Naled was implicated in a high-profile incident that killed millions of honey bees as a result of an aerial application in South Carolina in 2016 (Guarino 2021). Because honey bees are much larger in size than mosquitoes, this incident illustrates that lethal impacts from naled applications are not limited to small-bodied insects.

While studies have found minimal mortality of caged crickets in naled spray zones two hours after a single application by truck (Schleier & Peterson 2010) and very limited impacts to overall insect community composition after five aerial naled applications (Rochlin et al. 2022), Zhong et al. (2010) found increased mortality of Miami blue butterfly larvae and higher naled residues within naled spray zones compared to areas outside of spray zones. The chronic, sub-lethal and additive effects of naled remain a concern for the mysterious lantern firefly, particularly because the nocturnal flight of the firefly lines up with typical mosquito control spray times.

Mosquito larvicides: The DDNREC focuses early season efforts on the control of aquatic immature (larval) mosquitoes. This includes annual springtime (and some summer) aerial sprays of woodland pools, other freshwater wetlands, flooded woodlands, or coastal salt marshes or tidal wetlands, as

warranted. For example, in 2022, the Department indicated that up to 10,000 acres of wet woodlands near select populated areas would be treated by helicopter with *Bacillus thuringiensis* ssp. *israelensis* (Bti) to kill mosquito larvae beginning in southern Sussex County, then moving into Kent and New Castle Counties over several weeks. While Bti is likely not a large concern to the mysterious lantern firefly since it does not contain the proteins considered most toxic to coleopterans, other larvicides used by the Department, including methoprene (Altosid, Metalarv), *Bacillus sphaericus* (VectoLex), spinosad (Natular), and some larvicidal oils (CocoBear, BVA 2) are of greater concern (Delaware Department of Natural Resources and Environmental Control 2022f). In particular, spinosad and methoprene (an insect growth regulator) are two commonly used mosquito larvicides. Galvan et al. (2006) found that, when applied at maximum field rate, spinosad residues were toxic to nearly 40% of larval lady beetles (*H. axyridis*) within 2 days after treatment, although only about 10% of adults died when exposed to this treatment. Methoprene is toxic to beetle species in some situations (Liu et al. 2016). Potential negative impacts of mosquito larvicides on firefly larvae are concerning because of firefly larvae's smaller body size (than adults) and their use of moist habitats for foraging and shelter.

Pesticide impacts on larval food sources

Photuris larvae consume worms, snails, and slugs for their diet. Pesticide use that affects these prey species can reduce the food sources that larval fireflies need to develop and/or transmit high doses of pesticides to firefly larvae as they are consumed. Earthworms are also likely chronically exposed to chemicals such as neonicotinoids that persist in many soil types for months to years (Wood & Goulson 2017). Earthworms have been found to contain 200-700 ng/g of neonicotinoids when collected from treated fields (Douglas et al. 2015; Pelosi et al. 2021). Through exposure to environmentally relevant concentrations in soil, neonicotinoids have also been shown to damage earthworm DNA and to bioaccumulate relative to soil concentrations (Chevillot et al. 2017). Pelosi et al. (2021) found median imidacloprid concentrations in earthworms 22X higher than soil concentrations in cereal fields; a few herbicides and fungicides also showed bioaccumulation in earthworms. Other common pesticides—organochlorines, pyrazoles, carbamates, the herbicide 2,4-D, and certain fungicides—are also toxic to earthworms (Correia & Moreira 2010; Wang et al. 2012).

Snails, whether aquatic or terrestrial, consume plant material and algae, which may be affected by herbicides used in agriculture.

Atrazine is an herbicide and the second-most commonly used pesticide in the US (Atwood & Paisley-Jones 2017). Widely used on corn crops, atrazine is also applied frequently on the Delmarva Peninsula where *Photuris mysticalampas* occurs (Figure 8). Atrazine and related herbicides (metribuzin and diuron) degrade slowly in surface water with hydrolysis half-lives on the order of 30 days to more than 1 year (Schuler & Rand 2008). As a result of its widespread use and slow degradation, atrazine is one of the most frequently detected herbicides in surface waters across the U.S. (Ryberg & Gilliom 2015). Atrazine mimics estrogen in vertebrates, and at low levels has been associated with sublethal effects on invertebrates including disruption of sexual selection in the beetle *Tenebrio molitor* (McCallum et al. 2013) and altering hemocyte density and inhibition of hemocyte activity in freshwater pond snails

(Russo & Lagadic 2004). With its herbicidal activity, atrazine may also indirectly affect the abundance and distribution of aquatic plants and algae in the region, with potential impacts on the food sources of the mysterious lantern firefly.

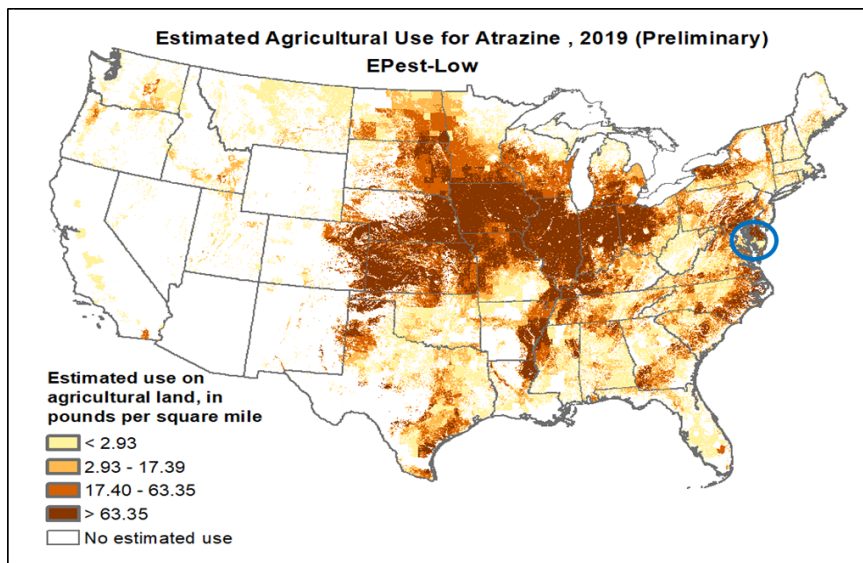


Figure 8. Preliminary lower-bound estimated agricultural application rates of the herbicide atrazine in the year 2019. Note that atrazine is heavily used within the known range of *Photuris mysticalampas* on the Delmarva Peninsula (blue circle). Map from U.S. Geological Survey Pesticide National Synthesis Project.

Other pollutants

More than 90% of Delaware's waterways are considered impaired. "Impaired waters" are severely polluted waters that do not meet water quality standards. The state's list of impaired waters, filed with the Environmental Protection Agency, includes bodies of water that suffer from 11 different impairments, the most common of which are pathogens (disease-causing bacteria and viruses) and nutrients (Delaware Department of Natural Resources and Environmental Control 2022g).

Nationwide, farmers applied nitrogen fertilizers to 97% of planted acres, at an average rate of 145 lbs. per acre (National Agricultural Statistics Service 2017), using phosphate, potassium and sulfur as well but in smaller quantities. The Nanticoke watershed suffers from elevated levels of nitrogen; report cards published by the Nanticoke Watershed Alliance indicate that a reduction in nitrogen loads is needed throughout the region, and the Broad Creek subwatershed scored an F in total nitrogen in the most recent report card (Nanticoke Watershed Alliance 2021), indicating high inputs and transport to aquatic systems in this subwatershed of the Nanticoke River.

The poultry industry was singled out for its nitrogen pollution loads entering Chesapeake Bay in a report by the Environmental Integrity Project (2020), with nitrogen loads originating from both manure and from ammonia emissions directly from the poultry houses. Ammonia emissions, which redeposit onto land and water, are directly toxic to aquatic life and subject to Clean Water Act standards. Overall nitrogen loads contributed by Sussex County (Delaware) are among the highest of all counties in the

Chesapeake Bay Basin. Lee et al. (2008) tested the effects of fertilizer ingredients on larvae of another species of firefly (*Luciola lateralis*) in the lab, finding that urea fertilizer and ammonium fertilizers resulted in 27% and 56% mortality of the tested subjects, respectively. Ridenhour (2022) found that fertilizer use in urban landscapes was associated with lower abundance of the firefly *Photinus pyralis* in the Atlanta, GA, metro area, with a stronger effect if fertilizer applications had occurred for three years or more. In the absence of research specifically on the mysterious lantern firefly, we hypothesize that nitrogen pollution would affect the mysterious lantern firefly in a manner similar to that of other studied firefly species.

Loss of prey

Declines in soft-bodied prey such as snails and slugs may further threaten the mysterious lantern firefly's existence. Firefly larvae are dependent on earthworms, terrestrial mollusks, and other soft-bodied invertebrates for food (Lewis 2016; Faust 2017). However, the same threats that the mysterious lantern firefly is facing are also being faced by its prey sources, including rising sea levels, pesticide use, and habitat degradation (Lydeard et al. 2004). For example, terrestrial mollusks are considered one of the most imperiled groups of animals on the planet (Lydeard et al. 2004). Currently, 21 species of land snails and 5 species of freshwater snails are listed as Species of Greatest Conservation Need in Delaware (Delaware Division of Fish and Wildlife 2015), and 14 species of land snail are listed as Species of Greatest Conservation Need in Maryland (Maryland Department of Natural Resources 2015). While the extent to which prey population trends are impacting firefly populations is unknown, it is clear that declines in local prey populations could have severe impacts on larval fireflies.

Small populations and the Allee effect

Fireflies have complex mating systems involving bioluminescent lighting displays, pheromones, and nuptial gifts (Lewis et al. 2004; Lewis & Cratsley 2008; Lewis 2016). As firefly sex ratio is near 1:1, any lack of males will result in lower female fecundity (Bauer et al. 2013). Small firefly populations due to habitat fragmentation and degradation can lower mating chances, an effect known as the Allee effect (Gascoigne et al. 2009; Bauer et al. 2013). For insects, if a population is demonstrating an Allee effect, populations may no longer be sustainable and can become extirpated (Gascoigne et al. 2009).

For fireflies, females need enough males in order to choose adequate mates to maximize fecundity and pass high quality genes onto offspring (Rooney & Lewis 2002; Lewis & Cratsley 2008; Bauer et al. 2013). Females can also benefit from more fit mates, by receiving nuptial gifts from males (Lewis & Cratsley 2008; Lewis 2016). Nuptial gifts are nutritious spermatophores that females can then use for survival and reproduction (Lewis & Cratsley 2008; Lewis 2016). Thus, females with more mate options and the ability to mate with more males will have higher fecundity, survival, and fitter offspring than females with reduced mate choices (Rooney & Lewis 2002; Lewis et al. 2004; Lewis & Cratsley 2008; South & Lewis 2012). Any loss in male population due to habitat degradation and fragmentation puts the mysterious lantern firefly at further risk of extinction due to lower reproductive output.

Request for critical habitat designation

We request that the Service designate critical habitat for the mysterious lantern firefly in concurrence with its listing. Critical habitat is defined in Section 3 of the ESA as “(i) the specific areas within the geographical area occupied by the species, at the time it is listed in accordance with the provisions of section 1533 of this title, on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed in accordance with the provisions of section 1533 of this title, upon a determination by the Secretary that such areas are essential for the conservation of the species” (16 U.S.C. § 1532 (5)).

A fundamental goal of the ESA is to conserve and protect “the ecosystems upon which endangered species and threatened species depend may be conserved.” 16 U.S.C. § 1531 (b). Thus, critical habitat is an effective and important component of the ESA, without which the mysterious lantern firefly’s chance for survival significantly diminishes. Petitioners therefore request that the Service propose critical habitat in concurrence with the species listing.

Conclusion

Fireflies are highly regarded among the public due to significant cultural, biological, and economic importance. The petitioners have carefully assessed the most current and accurate scientific information available for the mysterious lantern firefly regarding the threats this species has faced historically, faces presently, and will face in the future and have determined the species is in imminent danger of extinction throughout its range. The mysterious lantern firefly is a rare habitat specialist found in only six sites in two counties, one of which has not been confirmed as occupied in recent years (Fallon & Heckscher 2021; Firefly Atlas 2022; C. Heckscher pers. comm. 2022). The petitioners urge the listing of this imperiled species. The ESA requires that the Service promptly issue an initial finding as to whether this petition “presents substantial scientific or commercial information indication that the petitioned action may be warranted” 16 U.S.C. § 1533 (b)(3)(A).

The petitioners assess that the mysterious lantern firefly is warranted under the ESA as it is imperiled by 1) the present or threatened destruction, modification, or curtailment of its habitat or range; 4) the inadequacy of existing regulatory mechanisms; and 5) other natural or manmade factors affecting its continued existence as well as potential threats by 2) overutilization for commercial, recreational, scientific, or education purposes; and 3) disease or predation. The mysterious lantern firefly is imperiled by all five factors but most significantly by factors one, four, and five as evidenced by this petition. There are no existing regulations which are adequate to protect the mysterious lantern firefly. Listing the mysterious lantern firefly is the only way to provide continued existence for a species that would otherwise succumb to the combined threats of habitat degradation, light, pollution, climate change, and pesticides. A prompt decision is required to save this species from extinction.

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Literature Cited

- American Littoral Society. 2012. Assessing the impacts of Hurricane Sandy on coastal habitats. Report to the National Fish and Wildlife Foundation. Available from <https://crssa.rutgers.edu/projects/sandy/doc/ALS%20NFWF%20Final%20Assessment%20Report%20121712.pdf>.
- Armbrust KL, Peeler HB. 2002. Effects of formulation on the run-off of imidacloprid from turf. *Pest Management Science* **58**:702–706.
- Atwood D, Paisley-Jones C. 2017. Pesticides industry sales and usage: 2008-2012 market estimates. U.S. Environmental Protection Agency, Biological and Economic Analysis Division, Office of Pesticide Programs.
- Babendreier D, Jeanneret P, Pilz C, Toepfer S. 2015. Non-target effects of insecticides, entomopathogenic fungi and nematodes applied against western corn rootworm larvae in maize. *Journal of Applied Entomology* **139**:457–467.
- Bascom W. 1979. African Folktales in America VII. Inside Cow's (Elephant's) Belly. *Research in African Literatures* **10**:323–349. Indiana University Press.
- Bauer CM, Nachman G, Lewis SM, Faust LF, Reed JM. 2013. Modeling effects of harvest on firefly population persistence. *Ecological Modelling* **256**:43–52.
- Beachley M. 2008. Responses of non-target insects to mosquito abatement insecticide exposure in seasonal wetlands. California State University, Sacramento. Available from <https://csu-csus.esploro.exlibrisgroup.com/esploro/outputs/graduate/Responses-of-non-target-insects-to-mosquito/99257922061601671> (accessed February 17, 2023).
- Bonmatin J-M et al. 2015. Environmental fate and exposure; neonicotinoids and fipronil. *Environmental Science and Pollution Research* **22**:35–67.
- Branham MA, Faust LF. 2019. Firefly flashing activity during the totality phase of a solar eclipse. *Entomological News* **128**:191–203. The American Entomological Society.
- Buschman LL. 1984. Larval biology and ecology of *Photuris* fireflies (Lampyridae: Coleoptera) in northcentral Florida. *Journal of the Kansas Entomological Society* **57**:7–16. Kansas (Central States) Entomological Society.
- Chevillot F, Convert Y, Desrosiers M, Cadoret N, Veilleux É, Cabana H, Bellenger J-P. 2017. Selective bioaccumulation of neonicotinoids and sub-lethal effects in the earthworm *Eisenia andrei* exposed to environmental concentrations in an artificial soil. *Chemosphere* **186**:839–847.
- Correia FV, Moreira JC. 2010. Effects of glyphosate and 2,4-D on earthworms (*Eisenia foetida*) in Laboratory Tests. *Bulletin of Environmental Contamination and Toxicology* **85**:264–268.
- Coxe R. 2013. Guide to Delaware vegetation communities. Delaware Division of Fish and Wildlife. Available from <https://www.wrc.udel.edu/wp-content/heritage/NVCS/Guide-to-Delaware-Vegetation-Communities-Winter-2013.3.pdf>.
- Crop Life Foundation. 2013. The role of seed treatment in modern U.S. crop production: A review of benefits. Page 72. Washington, DC. Available from <https://croplifefoundation.wordpress.com/2013/12/06/the-role-of-seed-treatment-in-modern-u-s-crop-production/> (accessed February 17, 2023).
- De Cock R. 2009. Biology and behaviour of European lampyrids. *Bioluminescence in Focus: a Collection of Illuminating Essays*:163–200.
- De Cock R, Faust L, Lewis S. 2014. Courtship and mating in *Phausis reticulata* (Coleoptera: Lampyridae): Male flight behaviors, female glow displays, and male attraction to light traps. *Florida Entomologist* **97**:1290–1307. Florida Entomological Society.
- de Perre C, Murphy TM, Lydy MJ. 2015. Fate and effects of clothianidin in fields using conservation practices. *Environmental Toxicology and Chemistry* **34**:258–265.

- Delaware Coastal Programs. 2012. Preparing for tomorrow's high tide: A mapping appendix to the Delaware sea level rise vulnerability assessment. Delaware Department of Natural Resources and Environmental Control.
- Delaware Department of Natural Resources and Environmental Control. 2022a. Scientific collection permits. Available from <https://dnrec.alpha.delaware.gov/fish-wildlife/scientific-collection-permits>.
- Delaware Department of Natural Resources and Environmental Control. 2022b. Wildlife area maps and regulations. Available from <https://dnrec.alpha.delaware.gov/fish-wildlife/wildlife-areas/>.
- Delaware Department of Natural Resources and Environmental Control. 2022c. Nanticoke Watershed wetland assessment. Available from <https://dnrec.alpha.delaware.gov/watershed-stewardship/wetlands/assessments/nanticoke>.
- Delaware Department of Natural Resources and Environmental Control. 2022d. Delaware Mosquito Control Section. Available from <https://dnrec.maps.arcgis.com/apps/webappviewer/index.html?id=91e67ef755914218af05429242174d62>.
- Delaware Department of Natural Resources and Environmental Control. 2022e. Mosquito Control Spraying Calendar. Available from <https://dnrec.alpha.delaware.gov/fish-wildlife/mosquito-control/spray-calendar/>.
- Delaware Department of Natural Resources and Environmental Control. 2022f. DNREC Mosquito Control Section to begin spraying woodland pools. Available from <https://news.delaware.gov/2022/03/14/179297/>.
- Delaware Department of Natural Resources and Environmental Control. 2022g. State of Delaware 2022 combined watershed assessment report (305(b)) and determination for Clean Water Act Section 303(d) list of waters needing TMDLs (the Integrated Report). Available from <https://documents.dnrec.delaware.gov/Watershed/Assessment/Reports/2022-Delaware-Final-IR-with-appendices.pdf>.
- Delaware Division of Fish and Wildlife. 2015. Delaware Wildlife Action Plan. Delaware Department of Natural Resources and Environmental Control. Available from <https://dnrec.alpha.delaware.gov/fish-wildlife/conservation/wildlife-action-plan/> (accessed February 17, 2023).
- Disque HH, Hamby KA, Dubey A, Taylor C, Dively GP. 2019. Effects of clothianidin-treated seed on the arthropod community in a mid-Atlantic no-till corn agroecosystem. *Pest Management Science* **75**:969–978.
- Douglas MR, Rohr JR, Tooker JF. 2015. Neonicotinoid insecticide travels through a soil food chain, disrupting biological control of non-target pests and decreasing soya bean yield. *Journal of Applied Ecology* **52**:250–260.
- Druart C, Millet M, Scheifler R, Delhomme O, Raeppl C, de Vauflery A. 2011. Snails as indicators of pesticide drift, deposit, transfer and effects in the vineyard. *The Science of the Total Environment* **409**:4280–4288.
- Eisner T, Goetz MA, Hill DE, Smedley SR, Meinwald J. 1997. Firefly “femmes fatales” acquire defensive steroids (lucibufagins) from their firefly prey. *Proceedings of the National Academy of Sciences* **94**:9723–9728. *Proceedings of the National Academy of Sciences*.
- Eisner T, Wiemer DF, Haynes LW, Meinwald J. 1978. Lucibufagins: Defensive steroids from the fireflies *Photinus ignitus* and *P. marginellus* (Coleoptera: Lampyridae). *Proceedings of the National Academy of Sciences of the United States of America* **75**:905–908.
- Environmental Integrity Project. 2020. Poultry industry pollution in the Chesapeake Region: Ammonia air emissions and nitrogen load higher than EPA estimates. Page 48.
- Environmental Protection Agency. 2016. Characteristic Mid-Atlantic wetland type - White Cedar Swamp | Mid-Atlantic Wetlands | US EPA. Available from https://archive.epa.gov/reg3esd1/archive/web/html/white_cedar_swamp.html (accessed February 17, 2023).

- Evans TR, Salvatore D, van de Pol M, Musters C j. m. 2019. Adult firefly abundance is linked to weather during the larval stage in the previous year. *Ecological Entomology* **44**:265–273.
- Fallon CE, Heckscher CM. 2021. *Photuris mysticalampas*. The IUCN Red List of Threatened Species 2021: e.T164045835A166771508. IUCN Red List of Threatened Species. Available from <https://www.iucnredlist.org/en> (accessed February 17, 2023).
- Fallon CE, Walker AC, Lewis S, Cicero J, Faust L, Heckscher CM, Pérez-Hernández CX, Pfeiffer B, Jepsen S. 2021. Evaluating firefly extinction risk: Initial red list assessments for North America. *PLOS ONE* **16**:e0259379. Public Library of Science.
- Faust L. 2017. Fireflies, glow-worms, and lightning bugs: Identification and natural history of the fireflies of the eastern and central United States and Canada. University of Georgia Press, Athens, GA.
- Faust LF. 2010. Natural history and flash repertoire of the synchronous firefly *Photinus carolinus* (Coleoptera: Lampyridae) in the Great Smoky Mountains National Park. *Florida Entomologist* **93**:208–217. Florida Entomological Society.
- Faust LF, Davis J. 2019. A new species of *Photuris* Dejean (Coleoptera: Lampyridae) from a Mississippi cypress swamp, with notes on its behavior. *The Coleopterists Bulletin* **73**:97–113. The Coleopterists Society.
- Faust LF, Weston PA. 2009. Degree-day prediction of adult emergence of *Photinus carolinus* (Coleoptera: Lampyridae). *Environmental Entomology* **38**:1505–1512.
- Ferreira VS, Keller O, Ivie MA. 2022. Descriptions of new species of *Chespirito* Ferreira, Keller & Branham (Coleoptera: Lampyridae: Chespiritoinae) and the first record for the subfamily in the United States. *Zootaxa* **5124**:230–237.
- Firebaugh A, Haynes KJ. 2019. Light pollution may create demographic traps for nocturnal insects. *Basic and Applied Ecology* **34**:118–125.
- Firefly Atlas. 2022. Observation: *Photuris mysticalampas*. Available from https://www.fireflyatlas.org/firefly_observation/35733.
- Fireflyers International Network. 2014. Selangor Declaration. Available from <https://fireflyersinternational.net/selangor-declaration>.
- Flesher J. 2022. Backyard mosquito spraying booms, but may be too deadly. Available from <https://phys.org/news/2022-08-backyard-mosquito-booms-deadly.html> (accessed February 17, 2023).
- Forman RTT, Boerner RE. 1981. Fire frequency and the pine barrens of New Jersey. *Bulletin of the Torrey Botanical Club* **108**:34–50. Torrey Botanical Society.
- Galvan TL, Koch RL, Hutchison WD. 2006. Toxicity of indoxacarb and spinosad to the multicolored Asian lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), via three routes of exposure. *Pest Management Science* **62**:797–804.
- Gardiner T, Didham RK. 2020. Glowing, glowing, gone? Monitoring long-term trends in glow-worm numbers in south-east England. *Insect Conservation and Diversity* **13**:162–174.
- Gascoigne J, Berec L, Gregory S, Courchamp F. 2009. Dangerously few liaisons: A review of mate-finding Allee effects. *Population Ecology* **51**:355–372.
- Guarino B. 2021, October 25. ‘Like it’s been nuked’: Millions of bees dead after South Carolina sprays for Zika mosquitoes. *Washington Post*. Available from <https://www.washingtonpost.com/news/morning-mix/wp/2016/09/01/like-its-been-nuked-millions-of-bees-dead-after-south-carolina-sprays-for-zika-mosquitoes/> (accessed March 13, 2023).
- Hagen O, Santos RM, Schlindwein MN, Viviani VR. 2015. Artificial night lighting reduces firefly (Coleoptera: Lampyridae) occurrence in Sorocaba, Brazil. *Advances in Entomology* **3**:24–32. Scientific Research Publishing.
- Heckscher CM. 2013. *Photuris mysticalampas* (Coleoptera: Lampyridae): A new firefly from peatland floodplain forests of the Delmarva Peninsula. *Entomological News* **123**:93–100. The American Entomological Society.

- Heckscher CM. 2021. Four new species of North American fireflies from isolated peatlands with reference to species determination of *Photuris* Dejean (Coleoptera: Lampyridae). *Northeastern Naturalist* **28**:277–295. Eagle Hill Institute.
- Hennessey MK, Nigg HN, Habeck DH. 1992. Mosquito (Diptera: Culicidae) adulticide drift into wildlife refuges of the Florida Keys. *Environmental Entomology* **21**:714–721.
- Hitaj C, Smith DJ, Code A, Wechsler S, Esker PD, Douglas MR. 2020. Sowing uncertainty: What we do and don't know about the planting of pesticide-treated seed. *BioScience* **70**:390–403.
- Hladik ML, Bradbury S, Schulte LA, Helmers M, Witte C, Kolpin DW, Garrett JD, Harris M. 2017. Neonicotinoid insecticide removal by prairie strips in row-cropped watersheds with historical seed coating use. *Agriculture, Ecosystems & Environment* **241**:160–167.
- Hladik ML, Kolpin DW, Kuivila KM. 2014. Widespread occurrence of neonicotinoid insecticides in streams in a high corn and soybean producing region, USA. *Environmental Pollution* **193**:189–196.
- ITIS. 2023. ITIS - Report: *Photuris mysticalampas*. Available from https://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=952409#null (accessed March 9, 2023).
- Jackson D, Luukinen B, Gervais J, Buhl K, Stone D. 2011. d-Phenothrin technical fact sheet. National Pesticide Information Center, Oregon State University Extension Services. Available from <http://npic.orst.edu/factsheets/archive/dphentech.html>.
- Khoo V, Nada B, Kirton LG, Chooi-Khim P. 2009. Monitoring the population of the firefly *Pteroptyx tener* along the Selangor River, Malaysia for conservation and sustainable ecotourism. *Lampyrid* **2**:162–173.
- Knoepp JD, Vose JM, Michael JL, Reynolds BC. 2012. Imidacloprid movement in soils and impacts on soil microarthropods in Southern Appalachian eastern hemlock stands. *Journal of Environmental Quality* **41**:469–478.
- Kreutzweiser D, Good K, Chartrand D, Scarr T, Thompson D. 2007. Non-target effects on aquatic decomposer organisms of imidacloprid as a systemic insecticide to control emerald ash borer in riparian trees. *Ecotoxicology and Environmental Safety* **68**:315–325.
- Kuechle KJ, Webb EB, Mengel D, Main AR. 2019. Factors influencing neonicotinoid insecticide concentrations in floodplain wetland sediments across Missouri. *Environmental Science & Technology* **53**:10591–10600. American Chemical Society.
- Kynetec. 2019. AgroTrak survey. Kynetec Group, Newbury, United Kingdom. Available from <https://www.kynetec.com/solutions/agriculture>.
- Laderman AD. 1989. The ecology of Atlantic white cedar wetlands: A community profile. U.S. Fish and Wildlife Service Biological Report **85**:114.
- Latterell A. 2009. Prime Hook National Wildlife Refuge fire management plan approval. Available from <https://ecos.fws.gov/ServCat/DownloadFile/42058?Reference=42111>.
- Laurent EL, Ono K. 1999. The firefly and the trout: Recent shifts regarding the relationship between people and other animals in Japanese culture. *Anthrozoös* **12**:149–156. Routledge.
- Lauria M. 2022, May 9. "World class" mosquito habitat: Inside Delaware's war with biting insects. Available from <https://www.andrewsharp.net/why-delaware-does-mosquito-spraying-insecticides-and-more/> (accessed March 13, 2023).
- Lee K-Y, Kim Y-H, Lee J-W, Song M-K, Nam S-H. 2008. Toxicity of firefly, *Luciola lateralis* (Coleoptera: Lampyridae) to commercially registered insecticides and fertilizers. *Korean Journal of Applied Entomology* **47**:265–272. Korean Society of Applied Entomology.
- Lewis SM. 2016. *Silent sparks: The wondrous world of fireflies*. Princeton University Press, Princeton, NJ.
- Lewis SM et al. 2020. A global perspective on firefly extinction threats. *BioScience* **70**:157–167.
- Lewis SM et al. 2021. Firefly tourism: Advancing a global phenomenon toward a brighter future. *Conservation Science and Practice* **e391**. Available from <https://onlinelibrary.wiley.com/doi/10.1111/csp2.391> (accessed March 29, 2021).
- Lewis SM, Cratsley CK. 2008. Flash signal evolution, mate choice, and predation in fireflies. *Annual Review of Entomology* **53**:293–321.

- Lewis SM, Cratsley CK, Rooney JA. 2004. Nuptial gifts and sexual selection in *Photinus* fireflies. *Integrative and Comparative Biology* **44**:234–237. Oxford University Press.
- Lewis SM, Faust L, De Cock R. 2012. The dark side of the light show: Predators of fireflies in the Great Smoky Mountains. *Psyche*:e634027. Hindawi.
- Liu SS, Arthur FH, VanGundy D, Phillips TW. 2016. Combination of methoprene and controlled aeration to manage insects in stored wheat. *Insects* **7**:25.
- Lloyd JE. 1966. Studies on the flash communication system in *Photinus* fireflies. PhD dissertation. University of Michigan.
- Lloyd JE. 1973. Firefly parasites and predators. *The Coleopterists Bulletin* **27**:91–106. The Coleopterists Society.
- Lloyd JE. 2018. A naturalist's long walk among shadows of North American *Photuris*: Patterns, outlines, silhouettes... echoes. Bridgen Press.
- Long SM, Lewis S, Jean-Louis L, Ramos G, Richmond J, Jakob EM. 2012. Firefly flashing and jumping spider predation. *Animal Behaviour* **83**:81–86.
- Lumpkin T. 2020, January 23. Nature Conservancy intentionally sets fires to help with tree migration. Available from <https://www.wmdt.com/2020/01/nature-conservancy-intentionally-sets-fires-to-help-with-tree-migration/> (accessed March 13, 2023).
- Lydeard C et al. 2004. The global decline of nonmarine mollusks. *BioScience* **54**:321.
- Maryland Department of Natural Resources. 2015. Maryland State Wildlife Action Plan. Chapter 3: Maryland's Wildlife and Species of Greatest Conservation Need. Available from https://dnr.maryland.gov/wildlife/Documents/SWAP/SWAP_Chapter3.pdf.
- Maryland OneStop. 2023. Wildlife scientific collection permit. Available from <https://onestop.md.gov/licenses/wildlife-scientific-collection-permit-5d1540a654f24d03e9997ecb>.
- Mbugua SW, Wong CH, Ratnayake S. 2020. Effects of artificial light on the larvae of the firefly *Lamprigera* sp. in an urban city park, Peninsular Malaysia. *Journal of Asia-Pacific Entomology* **23**:82–85.
- McCallum ML, Matlock M, Treas J, Safi B, Sanson W, McCallum JL. 2013. Endocrine disruption of sexual selection by an estrogenic herbicide in the mealworm beetle (*Tenebrio molitor*). *Ecotoxicology* **22**:1461–1466.
- Michell PD. 2017. The value of pyrethroids in U.S. agricultural and urban settings. *AgInfomatics*. Available from https://aginfomatics.com/uploads/3/4/2/2/34223974/07_aginfomatics_pyrethroids_econassess_2017.pdf.
- Mullin CA, Saunders MC, Leslie TW, Biddinger DJ, Fleischer SJ. 2005. Toxic and behavioral effects to Carabidae of seed treatments used on Cry3Bb1- and Cry1Ab/c-protected corn. *Environmental Entomology* **34**:1626–1636.
- Nanticoke Watershed Alliance. 2021. 2020 Nanticoke River report card. Page 10.
- Nanticoke Watershed Alliance. n.d. Nanticoke River Watershed Management Plan. Page 72. Available from <https://docslib.org/doc/9423948/nanticoke-river-watershed-management-plan>.
- National Agricultural Statistics Service. 2017. 2016 agricultural chemical use survey: Corn. Page 2. No. 2017-2, NASS Highlights.
- National Oceanic and Atmospheric Administration. 2022. Coastal County Snapshots: Sussex County, DE. Available from <https://coast.noaa.gov/snapshots/#&state=eyJmaXBzljoiMTAwMDUiLCJzbnFwc2hvdEEljoiZnV0dXJI Rmxvbn2QiLCJzZWNOaW9uSUQiOiJhcHAtZm9vdGVyIiwic2xyVmFsdWUiOiIyIn0=>.
- Natural Resources Conservation Services. 2022a. Sussex County, Delaware: Soil type at 38.5633 -75.6767. Available from <https://websoilsurvey.nrcs.usda.gov/app/>.
- Natural Resources Conservation Services. 2022b. Wicomico County, Maryland: Soil type. Available from <https://websoilsurvey.nrcs.usda.gov/app/>.
- Natural Resources Conservation Services. 2022c. Sussex County, Delaware: Soil type at 38.835256 - 75.242785. Available from <https://websoilsurvey.nrcs.usda.gov/app/>.

- NatureServe. 2023. *Photuris mysticalampas* Heckscher, 2013. Available from https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.902376/Photuris_mysticalampas.
- Nowak P, Mitchell P, Hurley T. 2017. The value of pyrethroids in U.S. agricultural and urban settings. AgInformatics, LLC. Available from http://aginformatix.com/uploads/3/4/2/2/34223974/01_aginformatix_pyrethroid_execsum_2017.pdf.
- Oba Y, Schultz DT. 2022. Firefly genomes illuminate the evolution of beetle bioluminescent systems. *Current Opinion in Insect Science* **50**:100879.
- Owens ACS, Lewis SM. 2018. The impact of artificial light at night on nocturnal insects: A review and synthesis. *Ecology and Evolution* **8**:11337–11358.
- Owens ACS, Lewis SM. 2021. Effects of artificial light on growth, development, and dispersal of two North American fireflies (Coleoptera: Lampyridae). *Journal of Insect Physiology* **130**:104200.
- Owens ACS, Lewis SM. 2022. Artificial light impacts the mate success of female fireflies. *Royal Society Open Science* **9**:220468.
- Pearsons KA, Lower SE, Tooker JF. 2021a. Toxicity of clothianidin to common Eastern North American fireflies. *PeerJ* **9**:e12495.
- Pearsons KA, Rowen EK, Elkin KR, Wickings K, Smith RG, Tooker JF. 2021b. Small-grain cover crops have limited effect on neonicotinoid contamination from seed coatings. *Environmental Science & Technology* **55**:4679–4687. American Chemical Society.
- Peck DC. 2009. Comparative impacts of white grub (Coleoptera: Scarabaeidae) control products on the abundance of non-target soil-active arthropods in turfgrass. *Pedobiologia* **52**:287–299.
- Pelosi C et al. 2021. Residues of currently used pesticides in soils and earthworms: A silent threat? *Agriculture, Ecosystems & Environment* **305**:107167.
- Peterson RKD, Preftakes CJ, Bodin JL, Brown CR, Piccolomini AM, Schleier JJ. 2016. Determinants of acute mortality of *Hippodamia convergens* (Coleoptera: Coccinellidae) to ultra-low volume permethrin used for mosquito management. *PeerJ* **4**:e2167. PeerJ Inc.
- Picchi MS, Avolio L, Azzani L, Brombin O, Camerini G. 2013. Fireflies and land use in an urban landscape: the case of *Luciola italica* L. (Coleoptera: Lampyridae) in the city of Turin. *Journal of Insect Conservation* **17**:797–805.
- Pisa LW et al. 2015. Effects of neonicotinoids and fipronil on non-target invertebrates. *Environmental Science and Pollution Research* **22**:68–102.
- Popkin G. 2022. “Good fire” can help restore land in the East. Available from <https://www.motherjones.com/environment/2022/04/good-fire-can-help-restore-lands-in-the-eastern-us/> (accessed March 10, 2023).
- Radolinski J, Wu J, Xia K, Hession WC, Stewart RD. 2019. Plants mediate precipitation-driven transport of a neonicotinoid pesticide. *Chemosphere* **222**:445–452.
- Ridenhour K. 2022. Atlanta Firefly Project: Using community science to explore the effects of land management on the local abundance of the big dipper firefly (*Photinus pyralis*) in city parks and residential yards. Master of Science. University of Georgia. Available from <https://www.proquest.com/openview/6d01af56daf516c55810492c31304e5/1?pq-origsite=gscholar&cbl=18750&diss=y>.
- Rochlin I, White G, Reissen N, Martheswaran T, Faraji A. 2022. Effects of aerial adulticiding for mosquito management on nontarget insects: A Bayesian and community ecology approach. *Ecosphere* **13**. Available from <https://onlinelibrary.wiley.com/doi/10.1002/ecs2.3896> (accessed March 13, 2023).
- Rooney J, Lewis SM. 2002. Fitness advantage from nuptial gifts in female fireflies. *Ecological Entomology* **27**:373–377.
- Russo J, Lagadic L. 2004. Effects of environmental concentrations of atrazine on hemocyte density and phagocytic activity in the pond snail *Lymnaea stagnalis* (Gastropoda, Pulmonata). *Environmental Pollution* **127**:303–311.

- Ryberg KR, Gilliom RJ. 2015. Trends in pesticide concentrations and use for major rivers of the United States. *Science of The Total Environment* **538**:431–444.
- Schaafsma A, Limay-Rios V, Xue Y, Smith J, Baute T. 2016. Field-scale examination of neonicotinoid insecticide persistence in soil as a result of seed treatment use in commercial maize (corn) fields in southwestern Ontario. *Environmental Toxicology and Chemistry* **35**:295–302.
- Schleier JJ, Peterson RKD. 2010. Deposition and air concentrations of permethrin and naled used for adult mosquito management. *Archives of Environmental Contamination and Toxicology* **58**:105–111.
- Schuettler DJ. 2007. Fireflies in the night: Indigenous metaphor in Zapatista folktales. Union Institute and University. Available from <https://www.proquest.com/openview/01910a50b4243f57354edd2d86aff5f6/1?pq-origsite=gscholar&cbl=18750> (accessed March 9, 2023).
- Schuler LJ, Rand GM. 2008. Aquatic risk assessment of herbicides in freshwater ecosystems of South Florida. *Archives of Environmental Contamination and Toxicology* **54**:571–583.
- South A, Lewis SM. 2012. Effects of male ejaculate on female reproductive output and longevity in *Photinus* fireflies. *Canadian Journal of Zoology* **90**:677–681. NRC Research Press.
- Stanger-Hall KF, Lloyd JE. 2015. Flash signal evolution in *Photinus* fireflies: Character displacement and signal exploitation in a visual communication system. *Evolution* **69**:666–682.
- Stanger-Hall KF, Lloyd JE, Hillis DM. 2007. Phylogeny of North American fireflies (Coleoptera: Lampyridae): Implications for the evolution of light signals. *Molecular Phylogenetics and Evolution* **45**:33–49.
- State of Delaware. 2023. Title 7 – Conservation – Natural Resources – Chapter 71A. Regulation of Outdoor Lighting. Available from <https://delcode.delaware.gov/title7/c071a/index.html> (accessed February 6, 2023).
- Stehle S, Blin A, Bub S, Petschick LL, Wolfram J, Schulz R. 2019. Aquatic pesticide exposure in the U.S. as a result of non-agricultural uses. *Environment International* **133**:105234.
- Stone WW, Gilliom RJ, Ryberg KR. 2014. Pesticides in U.S. streams and rivers: Occurrence and trends during 1992–2011. *Environmental Science & Technology* **48**:11025–11030. American Chemical Society.
- Thancharoen A, Masoh S. 2019. Effect of camera illumination on flashing behavior of *Pteroptyx malaccae* (Coleoptera: Lampyridae) DOI: 10.5772/intechopen.85796. IntechOpen. Available from <https://www.intechopen.com/books/bioluminescence-analytical-applications-and-basic-biology/effect-of-camera-illumination-on-flashing-behavior-of-em-pteroptyx-malaccae-em-coleoptera-lampyridae> (accessed March 9, 2023).
- The Nature Conservancy. 2022. The Nanticoke River Watershed. Available from <https://www.nature.org/en-us/about-us/where-we-work/united-states/maryland-dc/stories-in-maryland-dc/nanticoke-river-watershed/>.
- Tiner RW. 2001. Delaware’s wetlands: Status and recent trends. Page 19. U.S. Fish and Wildlife Service, Northeast Region, Hadley, MA.
- Tiner RW. 2005. Assessing cumulative loss of wetland functions in the Nanticoke River watershed using enhanced National Wetlands Inventory data. *Wetlands* **25**:405–419.
- Tiner RW, Biddle M, Jacobs A, Rogerson A, McGuckin K. 2011. Delaware wetlands: Status and changes from 1992 to 2007. Cooperative National Wetlands Inventory Publication. U.S. Fish and Wildlife Service, Northeast Region, Hadley, MA and the Delaware Department of Natural Resources and Environmental Control, Dover, DE.
- Tiner RW, Burke DG. 1995. Wetlands of Maryland. U.S. Fish and Wildlife Service, Ecological Services, Region 5, Hadley, MA.
- Underwood TJ, Tallamy DW, Pesek JD. 1997. Bioluminescence in firefly larvae: A test of the aposematic display hypothesis (Coleoptera: Lampyridae). *Journal of Insect Behavior* **10**:365–370.
- United States Fish and Wildlife Service. 2022. Prime Hook National Wildlife Refuge. Available from <https://www.fws.gov/refuge/prime-hook>.

- Vance E, Kuri SR. 2017, August 24. How fireflies are keeping this tiny Mexican town alive. Available from <https://www.nationalgeographic.com/photography/article/firefly-fields-mexico-tourism-ecotourism> (accessed March 9, 2023).
- Wang Y, Cao C, Wang D. 2022. Physiological responses of the firefly *Pyrocoelia analis* (Coleoptera: Lampyridae) to an environmental residue from chemical pesticide imidacloprid. *Frontiers in Physiology* **13**. Available from <https://www.frontiersin.org/articles/10.3389/fphys.2022.879216> (accessed March 10, 2023).
- Wang Y, Wu S, Chen L, Wu C, Yu R, Wang Q, Zhao X. 2012. Toxicity assessment of 45 pesticides to the epigeic earthworm *Eisenia fetida*. *Chemosphere* **88**:484–491.
- Wilson R. 2007. Habitat assessment of the TNC Plum Creek Preserve – 2004 clear-cut area. Delmarva Botanical Surveys.
- Wilson R. 2009. Habitat assessment of the TNC Plum Creek Preserve – 2009 burn/clear-cut area. Delmarva Botanical Surveys.
- Wolfram J, Stehle S, Bub S, Petschick LL, Schulz R. 2018. Meta-analysis of insecticides in United States surface waters: Status and future implications. *Environmental Science & Technology* **52**:14452–14460. American Chemical Society.
- Wong C, Yeap CA. 2012. Conservation of congregating firefly zones (CFZs) in peninsular Malaysia. *Lampyrid* **2**:174–187.
- Wood TJ, Goulson D. 2017. The environmental risks of neonicotinoid pesticides: a review of the evidence post 2013. *Environmental Science and Pollution Research* **24**:17285–17325.
- Woods Jr. WA, Hendrickson H, Mason J, Lewis SM. 2007. Energy and predation costs of firefly courtship signals. *The American Naturalist* **170**:702–708. The University of Chicago Press.
- Zhong H, Hribar LJ, Daniels JC, Feken MA, Brock C, Trager MD. 2010. Aerial ultra-low-volume application of naled: Impact on nontarget imperiled butterfly larvae (*Cyclargus thomasi bethunebakeri*) and efficacy against adult mosquitoes (*Aedes taeniorhynchus*). *Environmental Entomology* **39**:1961–1972.