A Global Perspective on Firefly Extinction Threats

SARA M. LEWIS, CHOONG HAY WONG, AVALON C.S. OWENS, CANDACE FALLON, SARINA JEPSEN, ANCHANA THANCHAROEN, CHIAHSIUNG WU, RAPHAEL DE COCK, MARTIN NOVÁK, TANIA LÓPEZ-PALAFOX, VERONICA KHOO, AND J. MICHAEL REED

Insect declines and their drivers have attracted considerable recent attention. Fireflies and glowworms are iconic insects whose conspicuous bioluminescent courtship displays carry unique cultural significance, giving them economic value as ecotourist attractions. Despite evidence of declines, a comprehensive review of the conservation status and threats facing the approximately 2000 firefly species worldwide is lacking. We conducted a survey of experts from diverse geographic regions to identify the most prominent perceived threats to firefly population and species persistence. Habitat loss, light pollution, and pesticide use were regarded as the most serious threats, although rankings differed substantially across regions. Our survey results accompany a comprehensive review of current evidence concerning the impact of these stressors on firefly populations. We also discuss risk factors likely to increase the vulnerability of certain species to particular threats. Finally, we highlight the need to establish monitoring programs to track long-term population trends for at-risk firefly taxa.

Keywords: Coleoptera, extinction risk, insect conservation, IUCN, Lampyridae

Since their evolutionary origin some 297 million years ago (Zhang et al. 2018), beetles have been highly successful; they represent 38% of known insect species (Stork 2018). Fireflies (Coleoptera: Lampyridae) rank among the most charismatic beetles, with distinctive bioluminescent courtship displays that make them a potential flagship group for insect conservation. With more than 2000 species worldwide, firefly beetles exhibit surprisingly diverse life history traits (figure 1; Ohba 2004, Lloyd 2008, Lewis 2016), including nonluminous adults with daytime activity periods, glowworm fireflies with flightless females, and lightning bugs that exchange species-specific flash signals. Fireflies also inhabit ecologically diverse habitats, including wetlands (e.g., mangroves, rice paddies, marshes, desert seeps), grasslands, forests, agricultural fields, and urban parks. Their predaceous larvae, which can be aquatic, semiaquatic, or terrestrial, spend months to years feeding on snails, earthworms, and other soft-bodied prey. In contrast, firefly adults are typically short lived and do not feed. Some taxa are habitat and dietary specialists, whereas others are ecological generalists (Reed et al. 2020). Fireflies are economically important in many countries, because they represent a growing ecotourist attraction (Napompeth 2009, Lewis 2016). However, as is true for many invertebrates (Cardoso et al. 2011), fireflies have been largely neglected in global conservation efforts.

Monitoring studies that provide quantitative data on population trends are lacking for almost all firefly species. However, surveys have revealed significant recent declines in the mangrove firefly *Pteroptyx tener* in Malaysia (Jusoh and Hashim 2012, Khoo et al. 2014) and in the glowworm *Lampyris noctiluca* in England (Gardiner 2011, Atkins et al. 2017). Anecdotal reports and expert opinion also suggest reductions in both the occurrence and abundance of many firefly species over recent decades (Lewis 2016, Faust 2017, Lloyd 2018). In 2010, an international group of firefly experts convened in Malaysia and wrote *The Selangor Declaration on the Conservation of Fireflies* (Fireflyers International Network 2012), recommending actions to preserve these iconic insects. In 2018, the IUCN (International Union for Conservation of Nature) Firefly Specialist Group was established to assess the conservation status and extinction risks to fireflies worldwide. As part of this effort, in the present article we discuss perceived threats to firefly biodiversity and persistence on the basis of an opinion survey of experts from different geographic regions. We also review the current evidence for the impact of such threats on firefly populations. Finally, for each threat, we discuss associated risk factors (*sensu* Reed et al. 2020)—that is, behaviors and life history traits that make certain species especially vulnerable to particular threats.

A global survey of firefly experts

In January 2019, we sent a short Qualtrics survey (see box 1) by email to 350 people on the distribution list of the Fireflyers

BioScience 70: 157–167.
doi:10.1093/biosci/biz157
Advance Access publication 3 February 2020

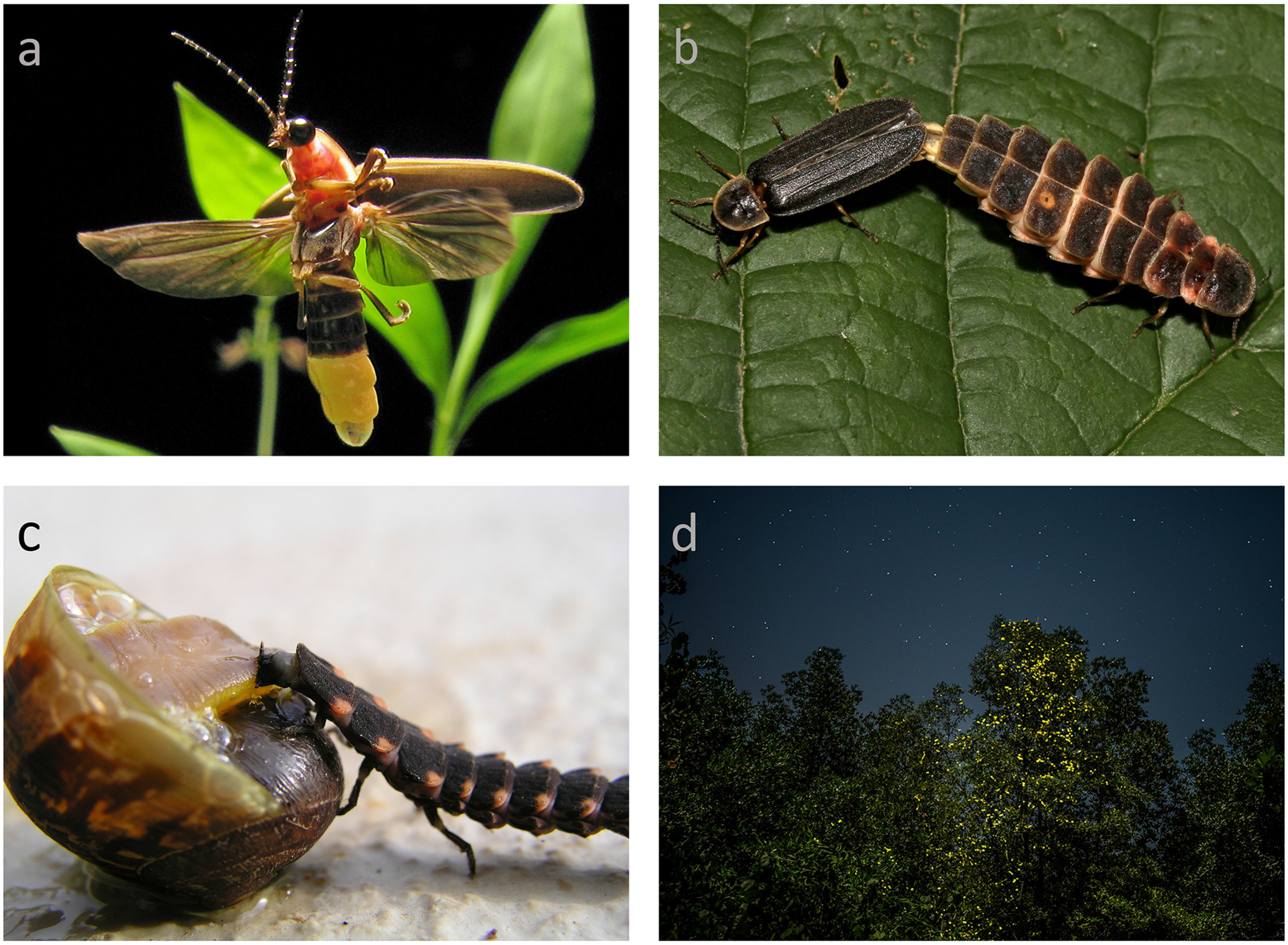

Figure 1. Firefly beetles (Coleoptera: Lampyridae) show great diversity in their ecology, behavior and extinction risk factors. (a) **Photinus pyralis** *adults of both sexes are capable of flight, but populations across the eastern United States still show restricted gene flow (photograph: Terry Priest). (b) Dispersal is even more limited in the glowworm fireflies such as* **Lampyris noctiluca***, whose females (right) are flightless (photograph: Zdeněk Chalupa). (c) All firefly larvae are predatory, and many are dietary specialists;* **L. noctiluca** *shown attacking* **Helix aspersa** *(photograph: Heinz Albers). (d) Massive courtship aggregations and synchronous flashing inspire ecotourism, which can lead to habitat degradation (***Pteroptyx malaccae** *in Thailand, photograph: Radim Schreiber).*

International Network, a scientific organization composed of individuals with interests and expertise in firefly ecology, behavior, taxonomy, or conservation. These survey results should be interpreted with caution, because they reflect only expert opinion concerning perceived threats to firefly species persistence.

We grouped the respondents into eight geographic regions: North America (United States, Canada), Central America and Mexico, Europe, South Asia (India, Sri Lanka), East Asia (Taiwan, Hong Kong, China, Japan), and Southeast Asia (Thailand, Malaysia). We had only single respondents each from Australia and South America and none from Africa. Using only those respondents who provided scores for all threats ($n = 49$), we present survey results as global threat scores averaged across the eight regions and the average threat scores by region. Comments by the respondents about specific threats are summarized below (see the supplemental material for detailed respondent comments). We also conducted a literature search for existing evidence concerning how these perceived threats influence firefly survival, reproduction, or population persistence. This information, in addition to comments by respondents about specific threats, is summarized below (see the supplemental material for detailed respondent comments).

The survey results

Habitat loss, artificial light, and pesticide use were identified as the three most serious threats when scores were averaged across the eight regions (table 1, figure 2). More than half of the 49 respondents assigned the

Box 1. The four survey questions.

Q1. What **country (or biogeographic region)** does your main firefly expertise cover?

Q2. In your country or region, how important is each of the following as a **current threat** to firefly populations? (Threats were presented in randomized order, and a 0–5 scale with a scoring resolution of 0.5 allowed for each threat.)

- Habitat loss
- Light pollution
- Pesticide use
- Overcollecting
- Water pollution
- Invasive species
- Climate change, sea level rise
- Climate change, drought
- Climate change, higher temperatures
- Climate change, storms and flooding

Q3. Are there **other current or future threats** to firefly populations in your country or region that we have **not** listed here? If so, please describe.

Q4. Thinking about the **two most important current threats,** can you describe how they affect a particular species or group of fireflies?

highest possible threat score (5) to habitat loss, whereas nearly one-third did so for light pollution, and one-fifth did so for pesticide use. However, their threat scores differed considerably across geographic regions (table 2, figure 2), with additional threats such as water pollution and tourism ranked as important concerns in some regions. Below, we provide details of the survey results, review the current evidence concerning the impact of each perceived threat, and propose risk factors that may interact with certain threats to increase the risk of population declines, local extirpation, or global extinction for particular firefly species.

Habitat loss and fragmentation

Habitat loss was perceived as the most serious threat to fireflies globally (table 1), as well as within nearly all regions (table 2). Habitat loss and fragmentation are predicted to be particularly problematic for habitat specialists (Reed et al. 2020). Genome-wide SNP (single nucleotide polymorphism) analysis of *Photinus pyralis*, a species widespread and abundant across the eastern United States, demonstrated low gene flow among populations, with Fst (fixation index) values averaging 0.38 (Lower et al. 2018). If this result is applicable to other firefly species, this degree of genetic isolation implies that extirpated populations are unlikely to be rescued by migration. Dispersal distances are even more limited in species with flightless females; this includes the glowworms *Lampyris noctiluca* (Atkins et al. 2017) and *Phosphaneus hemipterus;* in the latter, both sexes are flightless (De Cock 2009). Dispersal through larval movement may also be low: The estimated dispersal distance for the terrestrial larvae of *Luciola parvula* is only several meters during the entire larval period (Kakehashi et al. 2014). However, dispersal distances may be higher for species with aquatic larvae, because these might be transported along rivers and irrigation channels, as was reported for other aquatic macroinvertebrates (e.g., Perry and Perry 1986). In Thailand, eggs and larvae of the aquatic firefly *Sclerotia aquatilis* are often attached to duckweed and so may get transported along with this aquatic vegetation. If females or terrestrial larvae get transported by floods and survive in sufficient numbers, they may be able to colonize new patches of suitable habitat.

In Europe, firefly habitat has been lost through urbanization, industrialization, and agricultural intensification (De Cock 2009). Agricultural intensification—which entails habitat loss and fragmentation in addition to increased use of pesticides, herbicides, and fertilizer—has been identified as a major driver for declining populations of many insects (Wagner 2018, 2020). Throughout the United Kingdom, grassland habitats frequented by the glowworm *Lampyris noctiluca* have been lost to both agricultural intensification and woodland succession following the abandonment of pastureland (Gardiner 2011). Long-term surveys of *L. noctiluca* at several sites in southern and central England have documented significant population declines, possibly because of changes in land use (e.g., road construction, ditch filling, timber stockpiling), as well as drought (Gardiner 2011, Atkins et al. 2017). In Italy, one survey respondent considered agricultural intensification responsible for declining numbers of *Luciola italica*, *Luciola lusitanica*, and *Lampyris* fireflies on the Padana plain and the northern Appenines.

In contrast, another respondent in Mediterranean Spain expressed concern about the abandonment of small orchards and irrigated agricultural plots in which *Nyctophila reichii*, *Lampyris iberica*, and *Lamprohiza paulinoi* often occur. Once abandoned, these cultivated areas become more xeric and less suitable for snails, which constitute the main prey for certain fireflies.

Table 1. Scores averaged across regions (n = 8, equally weighted), and the percentage of all respondents who assigned each threat to fireflies either the highest (5) or the lowest (0) possible score.

	Habitat loss	Light pollution	Pesticide use	Water pollution	Climate change: Drought	Climate change: Higher temperatures	Climate change: Sea level rise	Climate change: Storms and flooding	Invasive species	Tourism	Overharvest
Global mean	4.28	3.62	3.29	1.84	1.98	1.98	1.78	1.78	1.22	1.49	0.91
Percentage scored 5	55.1	30.6	20.4	2.0	10.2	8.2	4.1	12.2	2.0	4.1	0
Percentage scored 0	2.0	2.0	8.2	26.5	24.5	26.5	28.6	22.4	32.7	22.4	32.7

Note: The threats to fireflies were scored on a scale from 0 to 5 by 49 respondents surveyed in January–February 2019.

In Japan, an iconic traditional landscape known as *satoyama* is disappearing in the face of development and rural out-migration (Kobori and Primack 2003). Composed of farming villages with streams, ponds, rice paddies, and cultivated fields surrounded by forest, this managed habitat once supported considerable biodiversity in the Japanese countryside, including fireflies (Oba et al. 2011).

In Malaysia, breeding congregations of *Pteroptyx tener* fireflies declined following conversion of riverbank mangroves to agriculture, aquaculture, and urbanization (Jusoh and Hashim 2012, Khoo et al. 2014). Throughout Southeast Asia, large areas of riverbank mangroves have been cleared for oil palm plantations, shrimp farms, or flood mitigation, making these sections unsuitable for the growth and development of *Pteroptyx* firefly larvae and their snail prey (Wong 2009, Nada et al. 2009, Thancharoen 2012, Wong and Yeap 2012, Jusoh and Hashim 2012, Jusoh et al. 2010, Khoo et al. 2012, 2014). In addition, *Pteroptyx* adults gather for nightly courtship displays in specific, prominent trees located along mangrove rivers, and many of these display trees have been removed (e.g., figure 3a).

The Atlantic rainforest of Brazil hosts high firefly biodiversity (Viviani 2001, Viviani and Santos 2012, Silveira and Mermudes 2013, 2014), but this is among the most threatened and fragmented rainforests worldwide (Hoorn et al. 2010). In Tlaxcala, Mexico, populations of *Macrolampis palaciosi* (another species with flightless adult females) are restricted to forest remnants fragmented by extensive logging (Vance and Kuri 2017). In eastern North America, the loss of firefly habitat occurs mainly through urbanization and commercial and residential development (e.g., figure 3b).

Globally, increasing human populations along coastlines have caused extensive habitat loss and fragmentation (Polidoro et al. 2010), threatening both mangrove fireflies and other species inhabiting coastal marshes. One such coastal habitat specialist in Delaware is *Photuris bethaniensis*, which is found in freshwater swales between oceanside dunes (Heckscher 2010); its wetland habitat faces imminent threat from extensive residential development (Kitt Heckscher, Delaware State University, Dover, Delaware, personal communication, 2018). In Florida, *Micronaspis floridana* inhabits intact coastal mangroves and salt marshes; this species' distribution is now quite restricted (Faust 2017). In the western United States and Texas, several fireflies are restricted to habitats adjoining permanent water sources, including rivers, streams, lakes, ponds, springs, and irrigated fields. Groundwater pumping to meet urban and agricultural water demands has substantially reduced surface water flow and lowered groundwater tables (Larry Buschman, Kansas State University, Lawrence, Kansas, personal communication, 2019), and increased drought due to climate change is likely to further diminish suitable firefly habitat in these areas.

Artificial light at night

Globally, artificial light at night (ALAN) was rated as the second most serious threat to fireflies (table 1). ALAN includes both direct lighting that affects a localized area (e.g., gas flares at petrochemical plants, streetlights, sports arenas, commercial signage, security lights, billboards) and skyglow, a more diffuse illumination that can exceed full-moon levels and can spread light far beyond urban centers. By conservative estimates, more than 23% of the global land surface now experiences some degree of artificial night sky brightness (Falchi et al. 2016). Light pollution was perceived as the top threat to fireflies in East Asia and South America and the second or third most serious threat in most other regions (table 2). ALAN is expected to be particularly problematic for nocturnally active firefly taxa, because these adults rely on bioluminescent courtship signals to locate mates (Lloyd 2008, Lewis 2009).

Observational and experimental studies provide evidence that ALAN adversely affects firefly populations (for a review, see Owens and Lewis 2018; also Mbugua et al. 2020). Several studies have shown negative correlations between high levels of ALAN and firefly abundance. For example, surveys showed that populations of *Luciola italica* were absent from the more brightly lit parts of the city of Turin, Italy (Picchi et al. 2013). Similarly, several different firefly species in São Paulo, Brazil, were restricted to areas with low levels of ALAN (Hagen and Viviani 2009, Viviani et al. 2010). Because ALAN is so tightly correlated with urbanization;

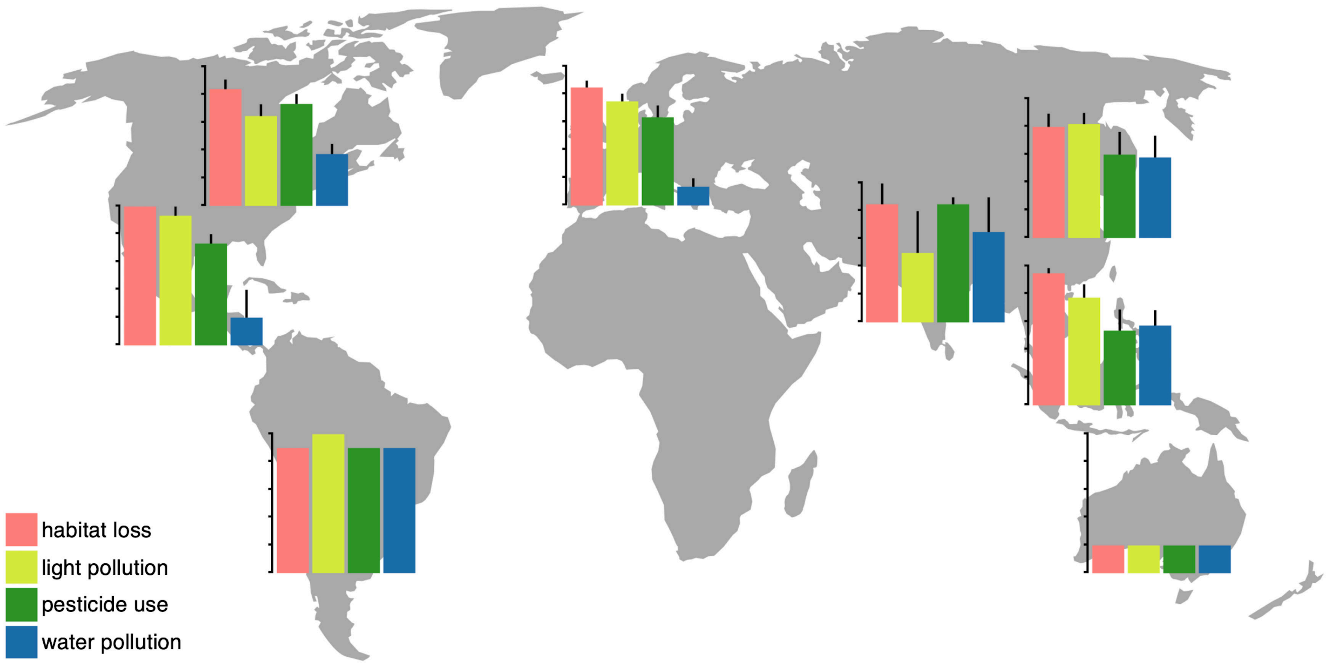

Figure 2. Geographic variation in scores for the four most serious threats to fireflies (bars show mean + one standard error, 0–5 scale) as reported by 49 respondents surveyed in January–February 2019. See table 2 for geographic regions, sample sizes, and scores for additional threats.

however, these observational studies make it difficult to isolate the primary cause of reduced firefly populations. In this context, local knowledge can be useful; one survey respondent cited increased light pollution around small and medium-size villages as responsible for declines in Spanish glowworms.

Owens and Lewis (2018) reviewed experimental studies demonstrating that artificial light interferes with the production and reception of firefly courtship signals. Females of the glowworm *Lampyris noctiluca* produce long-lasting glows to attract flying males, and several field studies show that various types of ALAN decrease male attraction (Ineichen and Rüttimann 2012, Bird and Parker 2014, Bek 2015). Many lightning bug fireflies engage in flash dialogs in which females give flash responses to male courtship signals (Lloyd 2008). ALAN has been shown to reduce courtship flashing by three lightning bug taxa: *Pteroptyx maipo* (Yiu 2012), *Photuris* (Firebaugh and Haynes 2016), and male *Photinus* (Hagen et al. 2015, Costin and Boulton 2016). Furthermore, *Photinus pyralis* females exposed to ALAN responded less often to male courtship signals (Firebaugh and Haynes 2016) and showed a nonsignificant reduction in mating success (Firebaugh and Haynes 2018). Therefore, several lines of evidence indicate that ALAN interferes with firefly reproductive behavior and may heighten extinction risk.

Pesticide use

Globally, pesticides were rated as the third most serious threat to fireflies (table 1), with some variation among geographic regions (table 2). Common agricultural insecticides include various organochlorines, organophosphates and, more recently, neonicotinoids (Simon-Delso et al. 2015). Although only a few studies have investigated their direct effects on fireflies (see below), such broad-spectrum insecticides are known to adversely affect numerous non-target insects and other taxa (reviewed by Sanchez-Bayo 2011, Pisa et al. 2015). Mechanisms of insecticide exposure include aerial spraying, contact with insecticide-containing soil or water, or ingestion of contaminated prey. For fireflies, high insecticide concentrations in water and soil may be particularly harmful, because the larval stage lives and develops for months to years either underwater (e.g., aquatic fireflies such as *Aquatica* and *Sclerotia*), among the roots of riparian mangroves and in vegetation behind adult display trees (*Pteroptyx* fireflies), or in soil (e.g., terrestrial fireflies such as *Lampyris*, *Photinus,* and *Photuris*). Other firefly life stages may also be exposed, because eggs are laid in soil, moss, or rotting wood, and pupae develop underground or on tree trunks. Adults may also be exposed to insecticide residues when resting on treated soil or foliage.

To date, the effects of direct exposure to pesticides on fireflies has been tested in only two published laboratory studies. Tabaru and colleagues (1970) reported that organophosphate insecticides (fenitrothion, fenthion, and difenphos) had low toxicity to Japanese *Luciola cruciata* larvae and their snail prey when tested as 5%–10% wettable powders, although fenthion 5% emulsifiable concentrate was toxic to both *L. cruciata* larvae and snails. In another

Table 2. Average scores and number of respondents grouped by geographic region.

Region	n	Habitat loss	Light pollution	Pesticide use	Water pollution	Climate change: Drought	Climate change: Higher temperatures	Climate change: Sea level rise	Climate change: Storms and flooding	Invasive species	Tourism	Overharvest
North America	15	4.00	3.23	3.67	1.87	2.73	2.20	1.50	2.77	1.93	1.27	1.10
Central America	3	5.00	4.67	3.67	1.00	1.00	2.67	0.17	1.17	1.00	1.83	1.00
South America	1	4.50	5.00	4.50	4.50	3.00	4.00	3.00	3.00	3.00	3.00	1.00
United Kingdom and Europe	14	4.25	3.75	3.18	0.68	1.67	1.50	0.75	0.75	0.79	0.46	0.39
East Asia	5	4.00	4.10	3.00	2.90	1.70	1.70	1.40	1.80	1.40	2.80	1.90
Southeast Asia	8	4.75	3.88	2.69	2.88	1.69	0.88	1.63	1.94	1.25	2.75	0.69
South Asia	2	4.25	2.50	4.25	3.25	1.25	1.25	1.25	1.50	1.50	2.00	0.75
Australia	1	1.00	1.00	1.00	1.00	3.00	3.00	1.00	1.00	1.00	1.00	1.00

Note: The threats to fireflies were scored on a scale from 0 to 5 by 49 respondents surveyed in January–February 2019.

study, conducted with Korean *Aquatica* (formerly *Luciola*) *lateralis*, ten insecticides were tested at their manufacturer recommended concentrations, and mortality increased to 80%–100% for both larvae and adults exposed to nine compounds, whereas egg hatchability dropped to 0%–33% for eight compounds (Lee et al. 2008). Tebufenozide caused 33% and 73% mortality of larvae and adults, respectively, but did not reduce egg hatchability; fipronil caused 83% larval and 100% adult mortality and reduced egg hatchability to 67%.

In Southeast Asia, agricultural runoff from oil palm plantations and shrimp farms poses hazards to fireflies that are aquatic or semiaquatic during their larval stage. A 2002–2003 study in the Selangor River in Malaysia found levels of several pesticides that sometimes exceeded acceptable limits for freshwater organisms (Leong et al. 2007). In Japan, industrial pollution and pesticide contamination of rivers has been implicated in the declining populations of *Luciola cruciata* and *Aquatica lateralis* that occurred during the second half of the twentieth century (Yuma 1993, Ohba 2004).

Although the European Union banned outdoor use of neonicotinoids in April 2018, in other regions, including the United States, these compounds continue to be widely used in both agricultural and residential settings (Bonmatin et al. 2015). In the United States, nearly all corn and soybean seeds are routinely coated with neonicotinoid insecticides (Douglas and Tooker 2015), which are persistent in most soils. In a field test conducted over a single growing season, corn plots planted with clothianidin-treated seed showed a 70.4% reduction in adult firefly abundance compared to control plots (Disque et al. 2018), most likely because of higher mortality of larvae in soil (Galen Dively, University of Maryland, College Park, Maryland, personal communication, 2019). Imidacloprid is a commonly used neonicotinoid marketed to homeowners for killing white grubs (larvae of Scarabaeidae beetles); in a 3-year study, the application of this pesticide as a lawn treatment greatly reduced the abundance of nontarget insects, including a 2.4-fold reduction in all other beetles (Peck 2009).

Insecticides such as pyrethroids are widely used for adult mosquito control but may also affect nontarget insects (Davis et al. 2007). Fireflies may be particularly at risk, because spraying is generally done at dusk, when mosquitoes and fireflies are both active. In field bioassays conducted with the beneficial lady beetle *Harmonia convergens*, ultra-low-volume application of permethrin caused high mortality for beetles contacted by the spray (Peterson et al. 2016).

Pesticides can also affect fireflies indirectly by reducing the availability or increasing toxicity of their larval prey, which include snails and earthworms. Imidacloprid and other neonicotinoids have been shown to be highly toxic to earthworms (for a review, see Sanchez-Bayo 2011, Pisa et al. 2015), which constitute the main prey for larval *Photinus* fireflies in North America (Lewis 2016). Earthworms and other prey can also bioaccumulate neonicotinoids (Douglas and Tooker 2015, Chevillot et al. 2017), representing an additional route for larval firefly exposure. Finally, lethal nontarget effects on firefly larvae have been observed for various biological control agents, including the fungi *Metarhizium* and *Beauvaria bassiana* and *Steinernema* sp. nematodes (Faust 2017; see the supplemental material).

Additional threats

In our survey, the remaining threats received lower average scores as they were given threat scores of 0 (meaning no threat) by 22%–33% of the respondents (table 1). However, the respondents in particular regions did highlight several other perceived threats to fireflies:

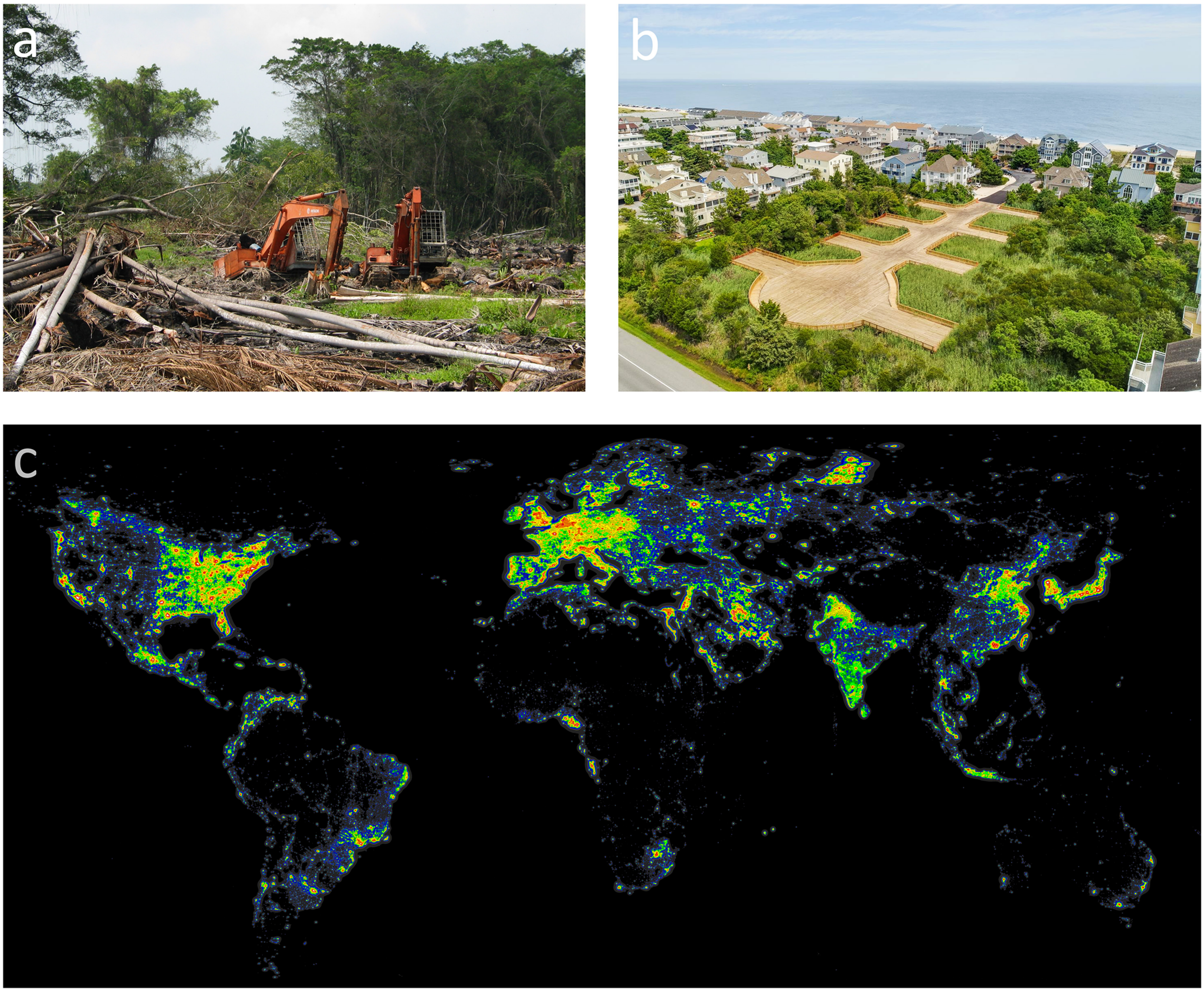

Figure 3. Among the top threats to fireflies globally are habitat loss and artificial light at night. (a) In Malaysia, clearing of riverbank mangroves along the Selangor River for agriculture and aquaculture destroys display trees used by Pteroptyx adults for courtship, and disturbs larval habitat (photograph: Laurence Kirton). (b) In Delaware, residential development threatens declining populations of **Photuris bethaniensis** *that are restricted to interdunal freshwater swales. (c) Global map of ALAN based on 2006 satellite data, colors indicate ratio of artificial to natural sky brightness: yellow represents 1–3 times brighter, orange represents 3–9 times brighter, red represents 9–27 times brighter. Map by David Lorenz, https://djlorenz.github.io/astronomy/lp2006.*

Water pollution. Across Asia and in South America, the respondents identified agricultural and industrial runoff containing fertilizers, pesticides, and other water-borne pollutants as the third or fourth most serious threat (table 2). In contrast to the mainly terrestrial larvae of Nearctic fireflies, numerous Asian fireflies have aquatic larvae that inhabit freshwater ponds, rivers, and streams, where they feed and develop through several larval instars (Lloyd 2008). This stage typically lasts for several months, during which both larvae and their snail prey will be exposed to water-borne pollutants.

Tourism. Firefly tourism has long been popular in Japan, Malaysia, and Taiwan, and similar recreational activity has recently been proliferating within other countries, including Thailand (Thancharoen 2012), the United States (Faust 2009, 2017), and Mexico (Vance and Kuri 2017). Collectively, firefly tourism attracts more than 200,000 visitors per year (Lewis 2016) and carries considerable economic benefits. However, if such tourism is not responsibly managed, it can threaten local firefly populations by disturbing larval and adult habitats and interfering with adult reproduction. Although many different fireflies produce attractive bioluminescence, most at risk are those that spontaneously synchronize; these species, such as *Photinus carolinus* in the United States, produce stunning displays in which hundreds of males flash rhythmically in unison. Throughout Southeast Asia, synchronous fireflies in the genus *Pteropytx* are a major tourist attraction because they congregate in large numbers in mangrove forests along tidal rivers (Wong and Yeap 2012). ALAN from commercial tour operations, flashlights, and even camera flashes (Thancharoen and Masoh 2019) can interfere with *Pteropytx* courtship behavior. In Thailand, *Pteropytx* tourism has generated high-speed motorboat traffic along mangrove rivers, resulting in riverbank erosion that topples display trees and destroys larval habitat. Other tourist-attracting fireflies have flightless females that may inadvertently get trampled by tourists as they signal from the ground or low vegetation; these include *Phausis reticulata* in North Carolina, and *Macrolampis palaciosi* in Nanacamilpa, Mexico.

Overharvest. Although not currently considered a threat, historically, the extensive harvest of fireflies from wild populations likely caused some population declines (Bauer et al. 2013). During the late nineteenth and early twentieth centuries, the Genji firefly, *Luciola cruciata*, was commercially harvested in Japan (Lewis 2017). In the United States, from 1960 until about 1995, Sigma Chemical Company annually harvested about three million North American fireflies to extract luciferase and luciferin (light-producing compounds; Lewis 2016). In China, between 2009 and 2017, millions of fireflies were harvested and sold online for theme park exhibitions and romantic gifts (Lewis and Owens 2017). Because of protests and letter-writing campaigns mounted by firefly conservation organizations, the commercial harvest of wild fireflies in China has been largely curtailed (Lei Ping, Firefly Ecological Alliance, Chengdu, China, personal communication, 2019).

Invasive species. Although most of the respondents did not rate exotic invasives as a major threat, the spread of *Solenopsis* fire ants across the southern United State could be an emerging threat, particularly for firefly species such as *Pyractomena borealis*, whose larvae are active aboveground (Lynn Faust, Emory River Land Company, Knoxville, Tennessee, personal communication, 2019).

Climate change. Although the effect of anthropogenic climate disruption on firefly populations remains unknown, the restricted ranges and specialized habitat requirements of certain fireflies suggest that they are likely to be threatened by drought and sea level rise (Reed et al. 2020). Fireflies require moist conditions throughout their life stages (Lloyd 2008, Atkins et al. 2017, Evans et al. 2018), so increased drought duration, frequency, or intensity—possibly in association with decreased snow cover—may extirpate local populations in some regions (but see supplemental table S1; Harris et al. 2019). For example, dry tropical montane regions (Wagner 2018, Janzen and Hallwachs 2019) may threaten the high diversity of fireflies in moist Neotropical forests. Similarly, in Australia and the western United States, where fireflies are restricted to areas with permanent water, drought may cause mortality either directly or by reducing larval food sources.

In Maryland and Delaware, *Photuris salina* is a habitat specialist that occupies the drier portion of coastal brackish and salt marshes, a habitat vulnerable to inundation from rising sea levels (Heckscher 2010). As was noted above, the Delaware coastal species *P. bethaniensis* is similarly vulnerable, because it occupies freshwater swales between coastal dunes within 500 meters of the Atlantic Ocean and less than 0.5 meters above the current sea level (Heckscher and Bartlett 2004). In Southeast Asia, several species of *Pteropytx* fireflies congregate in tall, visually prominent *Sonneratia caseolaris* mangrove trees, a species with low salt tolerance (Nada et al. 2009) that may be threatened by saltwater intrusion.

Moving forward

This article provides a global perspective concerning threats that may cause firefly population declines and that may increase extirpation or extinction risk. Our survey results elucidate what knowledgeable respondents judged to be the most important threats to firefly species persistence, revealing differences among various geographic regions. Although apparent that such opinions cannot be used to identify the relative importance or extent of such threats, our results are consistent with other assessments of the multifaceted causes for general declines in insect abundance and biodiversity (e.g., Leather 2018, Wagner 2018, 2020, Homburg et al. 2019). We believe this information will be useful for future studies aimed at understanding local drivers of firefly diversity and abundance. In addition, our literature review provides a comprehensive summary of the existing evidence about whether and how such threats affect firefly populations and describes risk factors likely to increase the vulnerability of certain firefly species to particular threats.

This perspective also highlights the urgent need to invest in monitoring studies that can provide long-term data to track trends in abundance and diversity for at-risk firefly species and sites. With a few notable exceptions, most evidence about firefly population trends is anecdotal, and work is needed to develop a set of standardized monitoring protocols. In addition, experimental studies are needed to characterize acute and chronic toxicity of common insecticides on firefly life stages.

Taking action

On the basis of this survey of perceived threats and our review of existing evidence for those threats' impacts on firefly populations, we make the following recommendations for actions to conserve these charismatic insects:

Preserve suitable habitat. We need to identify critically endangered species and establish sanctuaries that protect key firefly sites. In so doing, it is essential to consider the distinct habitat requirements of each life stage, thus ensuring suitable habitat for larvae and their prey, pupation sites, adult courtship displays, and female oviposition. Fireflies have the potential to serve as flagship species for establishing key biodiversity areas. In Malaysia, rapid loss of riverbank mangroves and adjacent land poses an ongoing threat to several species of *Pteroptyx* fireflies, an economically valuable ecotourist attraction. Therefore, identifying and preserving buffer zones adjacent to the riverbank will help ensure sustainable firefly populations and also support high wildlife diversity, including other invertebrates, plants, reptiles, mammals, and birds.

Control light pollution. To encourage successful mating by fireflies that rely on bioluminescent courtship signals, we need to minimize ALAN in and around their habitats. Ongoing studies are aimed at developing specific lighting recommendations, involving the tuning of light color (wavelength) and intensity, that will provide for public safety while promoting firefly reproduction. However, the diverse visual sensitivities of insects and other animals are likely to limit the effectiveness of color tuning to specific taxa. Reducing artificial light—both its extent and its duration—should, in contrast, benefit a wide range of culturally and economically important nocturnal animals.

Reduce insecticide use. Use of insecticides for cosmetic purposes such as on residential gardens, lawns, and public parks should be minimized. Most insecticide exposure occurs during larval stages, because firefly larvae spend months to years living in litter, belowground, or underwater. Although the direct impacts on fireflies have been examined in few studies, commonly used insecticides have adverse effects on a broad range of nontarget organisms, including other predaceous beetles and the prey consumed by larval fireflies.

Develop guidelines for sustainable tourism. Firefly tourism is proliferating worldwide and would benefit from recommendations about best practices for establishing and managing tourist sites. Such guidelines would outline ways to protect both larval habitat and adult display sites from disturbances that include trampling, light pollution, and pesticides.

Supplemental material

Supplemental data are available at *BIOSCI* online.

Acknowledgments

We thank all of the survey respondents for their input, with additional thanks to Larry Buschman, Ben Pfeiffer, and Lynn Faust for sharing their insights in great detail and to Sarah Hoyle for information on pesticide use. We are grateful to Pedro Cardoso and David Wagner for their detailed and thoughtful comments that greatly improved this manuscript. We are also grateful to Tufts University Department of Biology for administrative support.

References cited

Atkins V, et al. 2017. The status of the glow-worm Lampyris noctiluca L. (Coleoptera: Lampyridae) in England. Lampyrid 4: 20–35.

Bauer CM, Nachman G, Lewis SM, Faust LF, Reed JM. 2013. Modeling effects of harvest on firefly population persistence. Ecological Modelling 256: 43–52.

Bek RJ. 2015. Investigating the Impact of Artificial Night Lighting on the Common European Glow-Worm, Lampyris Noctiluca (L). Bachelor of science thesis, University of Leeds.

Bird S, Parker J. 2014. Low levels of light pollution may block the ability of male glow-worms (Lampyris noctiluca L.) to locate females. Journal of Insect Conservation 18: 737–743.

Bonmatin J-M, et al. 2015. Environmental fate and exposure; neonicotinoids and fipronil. Environmental Science and Pollution Research 22: 35–67.

Cardoso P, Erwin TL, Borges P, New TR. 2011. The seven impediments to invertebrate conservation and how to overcome them. Biological Conservation 144: 2647–2655.

Chevillot F, Convert Y, Desrosiers M, Cadoret N, Veilleux E, Cabana H, Bellenger J. 2017. Selective bioaccumulation of neonicotinoids and sublethal effects in the earthworm Eisenia andrei exposed to environmental concentrations in an artificial soil. Chemosphere 186: 839–847.

Costin KJ, Boulton AM. 2016. A field experiment on the effect of introduced light pollution on fireflies (Coleoptera: Lampyridae) in the Piedmont Region of Maryland. Coleopterists Bulletin 70: 84–86.

Davis RS, Peterson RKD, Macedo PA. 2007. An ecological risk assessment for insecticides used in adult mosquito management. Integrated Environmental Assessment and Management 3: 373–382.

De Cock R. 2009. Biology and behaviour of European lampyrids. Pages 161–200 in Meyer-Rochow VB, ed. Bioluminescence in Focus: A Collection of Illuminating Essays. Research Signpost.

Disque HH, Hamby KA, Dubey A, Taylor C, Dively GP. 2018. Effects of clothianidin-treated seed on arthropod community in a mid-Atlantic no-till corn agroecosystem. Pest Management Science 75: 969–978.

Douglas MR, Tooker JF. 2015. Large-scale deployment of seed treatments has driven rapid increase in use of neonicotinoid insecticides and preemptive pest managament in U.S. field crops. Environmental Science and Technology 49: 5088–5097.

Evans TR, Salvatore D, van De Pol M, Musters CJM. 2018. Adult firefly abundance is linked to weather during the larval stage in the previous year. Ecological Entomology 44: 265–273.

Falchi F, Cinzano P, Duriscoe D, Kyba CM, Elvidge CD, Baugh K, Portnov B, Rybnikova NA, Furgoni R. 2016. The new world atlas of artificial night sky brightness. Science Advances 2: e1600377.

Faust L. 2009. Synchronous firefly Photinus carolinus (Coleoptera: Lampyridae) of the Great Smoky Mountains National Park. Pages 126–140 in Napompeth B, ed. Proceedings of the 2008 International Symposium on Diversity and Conservation of Fireflies. Queen Sirikit Botanic Garden.

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.

Firebaugh A, Haynes KJ. 2016. Experimental tests of light-pollution impacts on nocturnal insect courtship and dispersal. Oecologia 182: 1203–1211.

Firebaugh A, Haynes KJ. 2018. Light pollution may create demographic traps for nocturnal insects. Basic and Applied Ecology 34: 118–125.

Fireflyers International Network. 2012. The Selangor declaration on the conservation of fireflies (revised 2014) Lampyrid 2: xi–xiii. https://fireflyersinternational.net/selangor-declaration.

Gardiner T. 2011. Glowing, Glowing, Gone? The Plight of the Glow-Worm in Essex. British Naturalists' Association.

Hagen O, Viviani VR. 2009. Investigation of the Artificial Night Lighting Influence in Firefly Occurrence in the Urban Areas of Campinas and Sorocaba Municipalities. Anais do IX Congresso de Ecologia do Brasil.

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.

Heckscher CM, Bartlett CR. 2004. Rediscovery and habitat associations of *Photuris bethaniensis* McDermott (Coleoptera: Lampyridae). Coleopterists Bulletin 58: 349–353.

Harris JE, Rodenhouse NL, Holmes RT. 2019. Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. Biological Conservation 240: 108219.

Heckscher CM. 2010. Delaware Photuris fireflies (Coleoptera: Lampyridae): New state records, conservation status, and habitat associations. Entomological News 121: 498–505.

Hoorn C, et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330: 927–931.

Homburg K, Drees C, Boutaud E, Nolte D, Schuett W, Zumstein P, von Ruschkowski E, Assmann T. 2019. Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in Northern Germany. Insect Conservation and Diversity 12: 268–277.

Ineichen S, Rüttimann B. 2012. Impact of artificial light on the distribution of the common European glow-worm, Lampyris noctiluca (Coleoptera: Lampyridae). Lampyrid 2: 31–36.

Janzen DH, Hallwachs W. 2019. Perspective: Where might be many tropical insects? Biological Conservation 233: 102–108.

Jusoh WFAW, Hashim NR. 2012. The effect of habitat modification on firefly populations at the Rembau-Linggi estuary, Peninsular Malaysia. Lampyrid 2: 149–155.

Jusoh WFA, Hashim NR, Ibrahim ZZ. 2010. Firefly distribution and abundance on mangrove vegetation assemblages in Sepetang estuary, Peninsular Malaysia. Wetlands Ecology and Management 18: 367–373.

Kakehashi K, Kuranishi RB, Kamata N. 2014. Estimation of dispersal ability responding to environmental conditions: Larval dispersal fo the flightless firefly Luciola parvula (Coleoptera: Lampyridae). Ecological Research 29: 779–787.

Khoo V, Nada B, Kirton L, Phon CK. 2012. Monitoring the population of the firefly Pteroptyx tener along the Selangor River, Malaysia for conservation and sustainable ecotourism. Lampyrid 2: 162–173.

Khoo V, Nada B, Kirton L. 2014. Conservation of the Selangor River population of Pteroptyx tener in Malaysia: Results of Seven Years of Monitoring. Forest Research Institute, Malaysia. https://conference.ifas.ufl.edu/firefly/Presentations/2%20-%20Wednesday/Session%206/0355%20Khoo.pdf.

Kobori H, Primack RB. 2003. Conservation for satoyama, the traditional landscape of Japan. Arnoldia 32: 307–311.

Leather SR. 2018. “Ecological Armageddon”: More evidence for the drastic decline of insect numbers. Annals of Applied Biology 172: 1–3.

Lee KY, Kim YH, Lee JW, Song MK, Nam SH. 2008. Toxicity of firefly, *Luciola lateralis* (Coleoptera: Lampyridae) to commercially registered insecticides and fertilizers. Korean Journal of Applied Entomology 47: 265–272.

Leong KH, Tan A, Mohd MA. 2007. Contamination levels of selected organochlorine and organophosphate pescticies in the Selangor River, Malaysia between 2002 and 2003. Chemosphere 66: 1153–1159.

Lewis SM. 2009. Bioluminescence and sexual signaling in fireflies. Pages 147–159 in Meyer-Rochow VB, ed. Bioluminescence in Focus: A Collection of Illuminating Essays. Research Signpost.

Lewis SM. 2016. Silent Sparks: The Wondrous World of Fireflies. Princeton University Press.

Lewis SM, Owens ACS. 2017. China’s Endangered Fireflies. Scientific American (11 September 2017). https://blogs.scientificamerican.com/observations/chinas-endangered-fireflies.

Lewis SM. 2017. For the Sake of Their Glow. Undark (1 June 2017). https://undark.org/article/sake-their-glow-moriyama-japan-fireflies.

Lloyd JE. 2008. Fireflies. Pages 1429–1452 in Capinera JL, ed. Encyclopedia of Entomology. Springer.

Lloyd JE. 2018. A Naturalist’s Long Walk among Shadows: of North American Photuris: Patterns, Outlines, Silhouettes… Echoes. Lloyd JE.

Lower SE, Stanger-Hall KF, Hall DW. 2018. Molecular variation across populations of a widespread North American firefly, *Photinus pyralis*, reveals that coding changes do not underlie flash color variation or associate visual sensitivity. BMC Evolutionary Biology 18: 129.

Nada B, Kirton LG, Norma-Rashid Y, Khoo V. 2009. Conservation efforts for the synchronous fireflies of the Selangor River in Malaysia. Pages 160–171 in Napompeth B, ed. Proceedings of the 2008 International Symposium on Diversity and Conservation of Fireflies. Queen Sirikit Botanic Garden.

Napompeth B, ed. 2009. Diversity and Conservation of Fireflies: Proceedings of the International Symposium on Fireflies. Queen Sirikit Botanic Garden.

Mbugua SW, Wong CH, Ratnayeke 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.

Oba Y, Branham M, Fukatsu T. 2011. The terrestrial bioluminescent animals of Japan. Zoological Science 28: 771–789.

Ohba N. 2004. Mysteries of Fireflies. Yokosuka City Museum.

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.

Peck D. 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.

Perry SA, Perry WB. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. Hydrobiologia 134: 171–182.

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 volumen permethrin used for mosquito management. PeerJ 4: e2167.

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 L, et al. 2015. Effects of neonicotinoids and fipronil on non-target invertebrates. Environmental Science and Pollution Research International 22: 68–102.

Polidoro BA, et al. 2010. The loss of species: Mangrove extinction risk and geographic areas of global concern. PLOS ONE 5 (art. e10095). doi:10.1371/journal.pone.0010095.

Reed JM, Nguyen A, Owens ACS, Lewis SM. 2020. Linking the seven forms of rarity to extinction threats and risk factors: An assessment of North American fireflies. Biodiversity Conservation 20: 57–75.

Sanchez-Bayo F. 2011 Pesticide impacts of agricultural pesticides on terrestrial ecosystems. Pages 63–87 in Sanchez-Bayo F, van den Brink PJ, Mann RM, eds. Ecological Impacts of Toxic Chemicals. Bentham Science.

Silveira LF, Mermudes JR. 2013. Memoan ciceroi gen. et sp. nov., a remarkable new firefly genus and species from the Atlantic rainforest (Coleoptera: Lampyridae). Zootaxa 3640: 79–87.

Silveira LF, Mermudes JR. 2014. Ybytyramoan, a new genus of fireflies (Coleoptera: Lampyridae, Lampyrinae, Photinini) endemic to the Brazilian Atlantic rainforest, with description of three new species. Zootaxa 3835: 325–337.

Simon-Delso N, et al. 2015. Systemic insecticides (neonicotinoids and fipronil): Trends, uses, mode of action and metabolites. Environmental Science and Pollution Research International 22: 5–34.

Stork NE. 2018. How many species of insects and other terrestrial arthropods are there on Earth? Annual Review of Entomology 63: 31–45.

Tabaru Y, Kouketsu T, Oba M, Okafuji S. 1970. Effects of some organophosphorus insecticides against the larvae of Genji firefly, Luciola cruciata and their prey, Japanese melanial snail Semisulcospira bensoni. Medical Entomology and Zoology 21: 178–181.

Thancharoen A. 2012. Well managed firefly tourism: A good tool for firefly conservation in Thailand. Lampyrid 2: 142–48.

Thancharoen A, Masoh S. 2019. Effect of Camera Illumination on Flashing Behavior of Pteroptyx Malaccae. InTechOpen. doi:10.5772/intechopen.85796

Vance E, Kuri SR. 2017. How Fireflies are Keeping this Tiny Mexican Town Alive. National Geographic, www.nationalgeographic.com/photography/proof/2017/08/firefly fields-mexico-tourism-ecotourism/.

Viviani VR. 2001. Fireflies (Coeloptera: Lampyridae) from southeastern Brazil: Habitats, life history, and bioluminescence. Annals of the Entomological Society of America 94: 129–145.

Viviani VR, Rocha MY, Hagen O. 2010. Fauna de besouros bio-luminescentes (Coleoptera: Elateroidea: Lampyridae; Phengodidae, Elateridae) nos municípios de Campinas, Sorocaba-Votorantim e Rio Claro-Limeira (SP, Brasil): Biodiversidade e influência da urbanização. Biota Neotropica 10: 103–116.

Viviani VR, Santos RMD. 2012. Bioluminescent Coleoptera of Biological Station of Boracéia (Salesópolis, SP, Brazil): Diversity, bioluminescence, and habitat distribution. Biota Neotropica 12: 21–34.

Wagner D. 2018. Trends in biodiversity: Insects. Pages 131–143 in DellaSala DA, Goldstein MI, eds. The Encyclopdia of the Anthropocene, vol. 3. Elsevier.

Wagner D. 2020. Insect declines in the Anthropocene. Annual Review of Entomology 65 (art. 011019-025151). doi:10.1146/annurev-ento-011019-025151

Wong CH. 2009. Firefly watching and consesrvation involving local communities in Malaysia. Pages 141–148 in Napompeth B ed. Proceedings of the 2008 International Symposium on Diversity and Conservation of Fireflies. Queen Sirikit Botanic Garden.

Wong CH, Yeap CA. 2012. Conservation of congregating firefly zones (CFZs) in Peninsular Malaysia. Lampyrid 2: 174–187.

Yiu V. 2012. Effects of artificial light on firefly flashing activity. Insect News 4: 5–9.

Yuma M. 1993. Hotaru no mizu, hito no mizu (Fireflies' Water, Human's Water). Shinhy-oron.

Zhang SQ, Che LH, Li Y, Liang D, Pang H, Ślipiński A, Zhang P. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. Nature Communications 9: 205. doi:10.1038/s41467-017-02644-4.

All authors are affiliated with the Firefly Specialist Group of the International Union for the Conservation of Nature Species Survival Commission (IUCN SSC). Sara M. Lewis (sara.lewis@tufts.edu), Avalon C.S. Owens, and J. Michael Reed are affiliated with the Department of Biology at Tufts University. Chiahsiung Wu is affiliated with Huafan University, in Taipei City, Taiwan. Choong Hay Wong is affiliated with the Malaysia Nature Society, in Kuala Lumpur, Malaysia. Candace Fallon and Sarina Jepsen are affiliated with The Xerces Society for Invertebrate Conservation, in Portland, Oregon. Anchana Thancharoen is affiliated with the Department of Entomology, in the Faculty of Agriculture, at Kasetsart University, in Bangkok, Thailand. Martin Novak is affiliated with the Department of Ecology at Czech University of Life Sciences in Prague, Czech Republic. Raphael De Cock is affiliated with the Department of Biology's Evolutionary Ecology Research Group at the University of Antwerp, in Belgium. Tania Lopez-Palafox is affiliated with the Instituto de Ecología at the Universidad Nacional Autónoma de México, in México City, México. Veronica Khoo is affiliated with the Forest Biodiversity Division of the Forest Research Institute Malaysia, in Selangor, Malaysia.