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REVIEW

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Firefly tourism: Advancing a global phenomenon toward a brighter future

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Abstract

Fireflies are charismatic beetles with attractive bioluminescent courtship displays that have recently been swept onto the global stage of nature tourism. Here, we provide the first comprehensive review of the geographic scope, magnitude, focal species, and other attributes of the major firefly tourism sites worldwide. Through targeted interviews and surveys, we estimate that in recent years over one million tourists travelled annually to sites located in at least 12 countries for firefly-watching. Rapid proliferation of firefly tourism provides a timely opportunity to examine how such activities may impact local firefly populations, and to highlight the biological factors that make certain

species especially vulnerable to tourism-associated threats. We offer science-based best practices for firefly ecotourism that can be tailored to fit local circumstances, including recommendations to: (1) Conserve the habitats required for all life stages to thrive, (2) involve local communities as key stakeholders, and (3) provide training programs for guides and interpretive materials for visitors. Finally, we provide suggestions for transforming tourist behavior to minimize impact on firefly populations. By developing management plans that incorporate these recommendations, firefly tourist sites can enhance the visitor experience, protect natural resources, benefit local communities, and help promote the conservation of invertebrate biodiversity.

KEYWORDS

biodiversity, community-based conservation, ecotourism, habitat degradation, insect conservation, invertebrates, Lampyridae, light pollution, tourism management, wildlife tourism

1 | INTRODUCTION

The World Tourism Organization (WTO) estimates that during 2018 some 1.4 billion tourists travelled internationally, a recreational activity that contributed more than USD 1,451 billion to the global economy (WTO, 2019). Within this context, nature tourism represents one of the most rapidly growing segments (Balmford et al., 2015; Ceballos-Lascurain, 2012). Nature tourists travel to destinations specifically to experience and enjoy nature in the form of beautiful landscapes, high biodiversity habitats and charismatic wildlife, primarily birds, mammals, and reptiles (Stronza & Durham, 2008). In a phenomenon dubbed entomotourism (Lemelin, 2013; Lemelin, Boileau & Russell, 2019), a variety of insects have also begun to garner attention from wildlife tourists. Each year millions of people visit glow-worm caves, butterfly pavilions, insect museums, monarch butterfly overwintering sites, and hives of *Melipona* stingless bees (Lemelin & Jaramillo-López, 2019; Samways, 2005).

The International Ecotourism Society (TIES, 2015) defines ecotourism as "responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education." Although definitions have proliferated since Ceballos-Lascurain (1996), a universal criterion is the potential for making a positive contribution to conservation of the natural environment (Buckley, 2009). Ecotourism aims to generate this positive impact through raising environmental awareness, enhancing financial, political and social support for protecting wildlife populations and habitats, and providing alternatives to more land-intensive practices and extractive industries (Stronza & Durham, 2008; Stronza, Hunt, & Fitzgerald, 2019; Wardle, Buckley, Shakeela, & Castley, 2018). Ecotourism also strives to generate economic benefits for local communities consistent with local cultural and social needs, including support to strengthen local institutions responsible for on-the-ground conservation management (Fennell 2008, Fennell, 2020; D'Souza et al., 2019).

Fireflies (beetles in the family Lampyridae) include about 2,200 species worldwide (Martin et al., 2019), and their breathtaking bioluminescent displays make them one of earth's most charismatic insects (Lewis, 2016; Oba, Branham, & Fukatsu, 2011; Ohba, 2004). Firefly tourism has a long history in East Asia, but this recreational activity has recently become a global phenomenon that risks overwhelming current management strategies at some locations (Faust, 2010, 2017; Thancharoen, 2012; Vance & Kuri, 2017). As representatives of the IUCN SSC Firefly Specialist Group, our goal in this article is to evaluate the current state of firefly tourism around the world, to describe its many benefits, and to identify conservation threats associated with firefly tourism's rapid growth. We also propose guidelines to promote more sustainable forms of firefly ecotourism that can provide both economic and conservation benefits.

2 | THREATS AND RISK FACTORS

Fireflies undergo complete metamorphosis, dramatically altering their morphology and ecological niche during the four stages of their life cycle (Figure 1a). All firefly larvae produce bioluminescence; the adults of many, though not all, species also generate light as a courtship signal (Branham & Wenzel, 2003; Lewis & Cratsley, 2008). Fireflies inhabit diverse habitats, including wetlands (e.g., ponds, streams, mangroves, marshes, and desert seeps), grasslands, and forests (Lloyd, 2002). Firefly

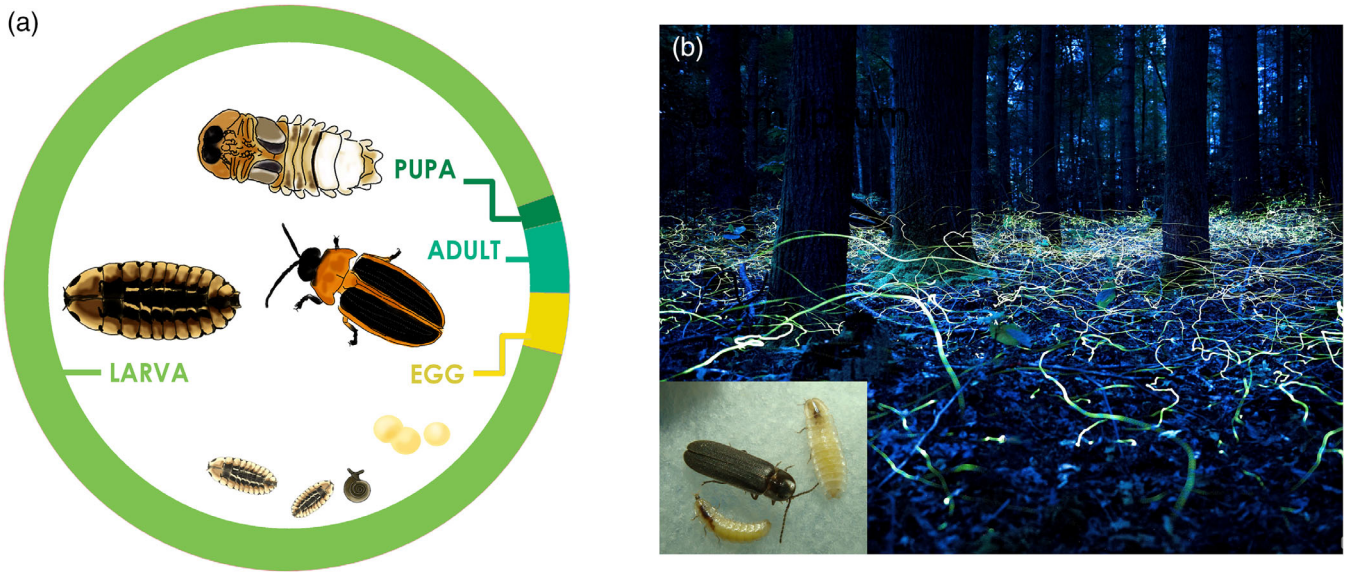

FIGURE 1 (a) Typical firefly life cycle illustrates long duration of the larval stage compared with relatively short-lived adults (*Asymmetricata circumdata* from Thailand, drawings by Anchana Thancharoen). (b) Like many fireflies, the blue ghost *Phausis reticulata* is highly sexually dimorphic: flying males emit a long-lasting glow (photo by Spencer Black), but the wingless, pale females live among leaf litter on the forest floor (inset photo by Raphael De Cock)

larvae are predaceous, consuming snails, earthworms, and other soft-bodied prey (Lloyd, 2008). These larvae require anywhere between a few months to several years to fully develop into adults. Adult activity revolves around courtship and reproduction: in most species, this non-feeding adult stage lasts only a few weeks. Thus, while the aerial adults are often marvelously conspicuous, the juveniles (i.e., the egg, larva, and pupa) actually constitute the longest portion of every firefly life cycle (Figure 1a). Depending on the species, firefly larvae can be terrestrial, semi-aquatic or fully aquatic (Lloyd, 2008; Ohba, 2004). In terrestrial firefly species, females lay their eggs in mud, leaf litter or moss, and larvae hunt for prey on or under the soil. Larvae of semi-aquatic species can hunt both above and underwater, while fully aquatic larvae have gills and develop in ponds, rice paddies, and rivers (Fu, Ballantyne, & Lambkin, 2012).

A recent global survey and review (Lewis et al., 2020) discussed the major threats to firefly persistence, which include loss and degradation of larval and adult habitats, disruption of adult courtship due to light pollution, and overuse of broad-spectrum insecticides. Although tourism did not emerge among the top threats globally, on a local scale tourism-related activities can have serious negative impacts. Tourism can impact firefly populations through degradation of the habitats where adult courtship takes place, as well as the habitats used for egg-laying, larval prey capture, growth and development, and pupation sites.

Most visibly, tourism could directly destroy or degrade firefly habitat during the construction of associated infrastructure, such as on-site tourist facilities, jetties, resorts, restaurants, and parking lots. But tourism may also lead indirectly to habitat degradation through soil compaction and erosion, disturbance of leaf litter, water pollution or light pollution (Buckley & Pannell, 1990). Trampling associated with heavy foot traffic causes soil compaction, litter fragmentation and erosion (Ceballos-Lascurain, 1996), and may alter plant communities and reduce prey availability. In southeast Asia, where tourists arrive by boat to view the fireflies that inhabit riverside mangrove forests, high levels of motorboat traffic can cause shoreline erosion as well as water pollution from gas and oil leakage (Bilkovic et al., 2017).

Tourism can also introduce light pollution (also called artificial light at night, or ALAN), which is known to disrupt firefly courtship signaling (reviewed by Owens & Lewis, 2018). Light pollution can emanate from stationary sources associated with infrastructure development, including commercial signage for tour operations, resorts, street and dock lighting, and restroom facilities. Firefly courtship can also be disrupted by portable lights such as headlights, boat lights, flashlights, and even cell phones and camera flashes (Thancharoen & Masoh, 2019).

Trampling may also reduce firefly survivorship directly by causing mortality of ground-dwelling life stages, which include eggs, larvae, and pupae. In about 25% of all firefly species worldwide, adult females are particularly vulnerable to trampling because they lack functional wings and thus cannot fly (e.g., the blue ghost firefly, *Phausis reticulata* Figure 1b, Lewis, 2016; Lloyd, 2008). In addition, heavy foot traffic can reduce

firefly reproductive success by disrupting mated pairs that perch on low vegetation and by inadvertently trampling females as they seek oviposition sites on the ground.

In addition to its ecological impact on fireflies and their habitat, poorly managed tourism can have negative social and cultural consequences. Whenever a site's visitation rates exceed its carrying capacity, overcrowding will diminish the visitor experience. Furthermore, rapidly rising tourist numbers can cause conflict among stakeholders by straining local infrastructure, including roads, rivers, and wastewater treatment systems (Borges, Bushell, Carbone, & Jaeger, 2011).

Using existing knowledge concerning firefly species' ecology and behavior, we can predict which traits and behaviors will make certain firefly species especially vulnerable to particular threats (Reed, Nguyen, Owens, & Lewis, 2020). In the context of the tourism threats described above, such risk factors (Table 1) include producing attractive bioluminescent courtship displays (e.g., quick flashes produced by adults of both sexes in lightningbugs or the longer-lasting emissions of glowworm fireflies sensu, Lewis, 2016; Lloyd, 2008), male flash synchrony, breeding congregations that are highly localized in space or time, and flightless adult females. As discussed below, the presence of any (and sometimes all) of these risk factors can magnify tourism's impact to increase the risk of population decline, local extirpation, or even global extinction for particular firefly species.

3 | THE BRIGHT SIDE

Although firefly tourism poses certain challenges, it also provides many tangible benefits. Firefly tourism can bring economic benefits in the form of employment and revenue across multiple levels, including local communities, states, nations, and regions. Firefly-watching offers an unforgettable experience, perhaps especially for city-dwellers who might otherwise have spent little time in nature. Fireflies are often viewed as romantic, and across many cultures they evoke happy childhood memories associated with former rural lifestyles (Haugan, 2019; Lewis, 2016). Visitors often describe powerful emotional responses to the luminous landscapes they see at firefly sites, reporting transformative experiences of delight and even spiritual awe (e.g., Faust, 2017; Lewis, 2016; Schreiber, 2017). People who venture out into the night to watch fireflies with family and friends may sometimes experience what the French sociologist of religion Émile Durkheim termed "collective effervescence" (Durkheim, 1912; Wood, 2019). Such firefly experiences may have long-lasting and widespread beneficial impacts, including not only improved mental health and well-being (Buckley et al., 2019), but also promoting more positive attitudes toward biodiversity conservation. Thus, these highly charismatic insects provide an alluring advertisement for protecting invertebrate biodiversity and for conservation philanthropy.

Many world cultures have a long history of appreciating the delights of firefly-watching. In Japan, where fireflies are woven tightly into the cultural fabric, admiring these insects has been a popular summertime activity for centuries (Kawahara, 2007; Laurent & Ono, 1999; Lewis, 2016; Oba et al., 2011). In the early 1900s, thousands of visitors boarded trains in Kyoto and Osaka to travel to Uji, a town famous for the splendid displays created by courting Genji fireflies (*Luciola cruciata*). During peak season in June, firefly boats made nightly cruises along the Ujiwara River, where

TABLE 1 Risk factors consist of life history traits and behaviors that make certain firefly species especially vulnerable to tourism-associated threats (after Reed et al., 2020)

Risk factors	Example taxa	Tourism locations
1. Adults produce attractive bioluminescence (flashes or glows)	*Luciola cruciata*, *Luciola parvula* *Aquatica ficta*, *Abscondita* spp.	Japan Taiwan
2. Adult males exhibit flash synchrony	*Photinus carolinus* *Photuris frontalis* *Photinus palaciosi*	USA (TN, NC, PA) USA (SC) Mexico (Tlaxcala, Estado de Mexico, Puebla)
3. Highly localized breeding congregations	*Pteroptyx* spp.	Malaysia, Thailand
4. Adult females are flightless	*Phausis reticulata* *Photinus palaciosi* *Diaphanes* spp., *Pyrocoelia* spp., *Lamprigera* spp. *Lampyris* spp., *Lamprohiza splendidula*, *Luciola lusitanica*, *L. italica*	USA (TN, NC) Mexico (Tlaxcala, Estado de México, Puebla) Taiwan Europe (Belgium, Portugal, Italy, Switzerland)

passengers could dine while enjoying the display (Allen & Wilson, 1992).

Firefly watching has a similarly long history in Thailand (Napompeth, 2009; Thancharoen, 2012). In 1685, a French priest reported thousands of flashing fireflies gathered in mangrove trees along tidal rivers near Bangkok. At night, males of these congregating fireflies (genus *Pteroptyx*) begin flashing in unison, maintaining their nearly precise synchrony all night long. The predictable location of these firefly display trees long served as navigational beacons for local boatmen as they navigated rivers at night. These remarkable displays were introduced to English-speaking audiences by zoologist H.M. Smith, who in 1935 penned a short communication for the journal *Science*: "Imagine a tree thirty-five to forty feet high thickly covered with small ovate leaves, apparently with a firefly on every leaf and all the fireflies flashing in perfect unison at the rate of about three times in 2 s, the tree being in complete darkness between flashes.... Imagine a tenth of a mile of river front with an unbroken line of [mangrove] trees with fireflies on every leaf flashing in synchronism, ... Then, if one's imagination is sufficiently vivid, he may form some conception of this amazing spectacle" (Smith, 1935, p. 151).

From these early beginnings, during the past few decades firefly tourism has taken off to become a popular

FIGURE 2 Examples of firefly tourism sites: (a) In Malaysia at Kampung Kuantan, tourists arrive year-round for boat tours along the mangrove river to watch synchronous congregating fireflies, *Pteroptyx tener* (Night Ride by Zol M: Flickr CC BY-NC-ND 2.0). (b) In Mexico at Nanacamilpa, between June and August tourists will follow guides into the forest to view courtship displays of synchronous roving fireflies *Photinus palaciosi* (photo by Tania López-Palafox). (c) In the Great Smoky Mountains National Park, USA tourists settle on chairs and spread blankets to watch displays of synchronous roving fireflies *Photinus carolinus* during their 2-week mating season (photo by Calvin Mattheis for Knoxville Sun Times). (d) Trained guides at Liyu Lake, Taiwan explain life cycles and species identification to visitors prior to firefly-watching (photo by Sara Lewis)

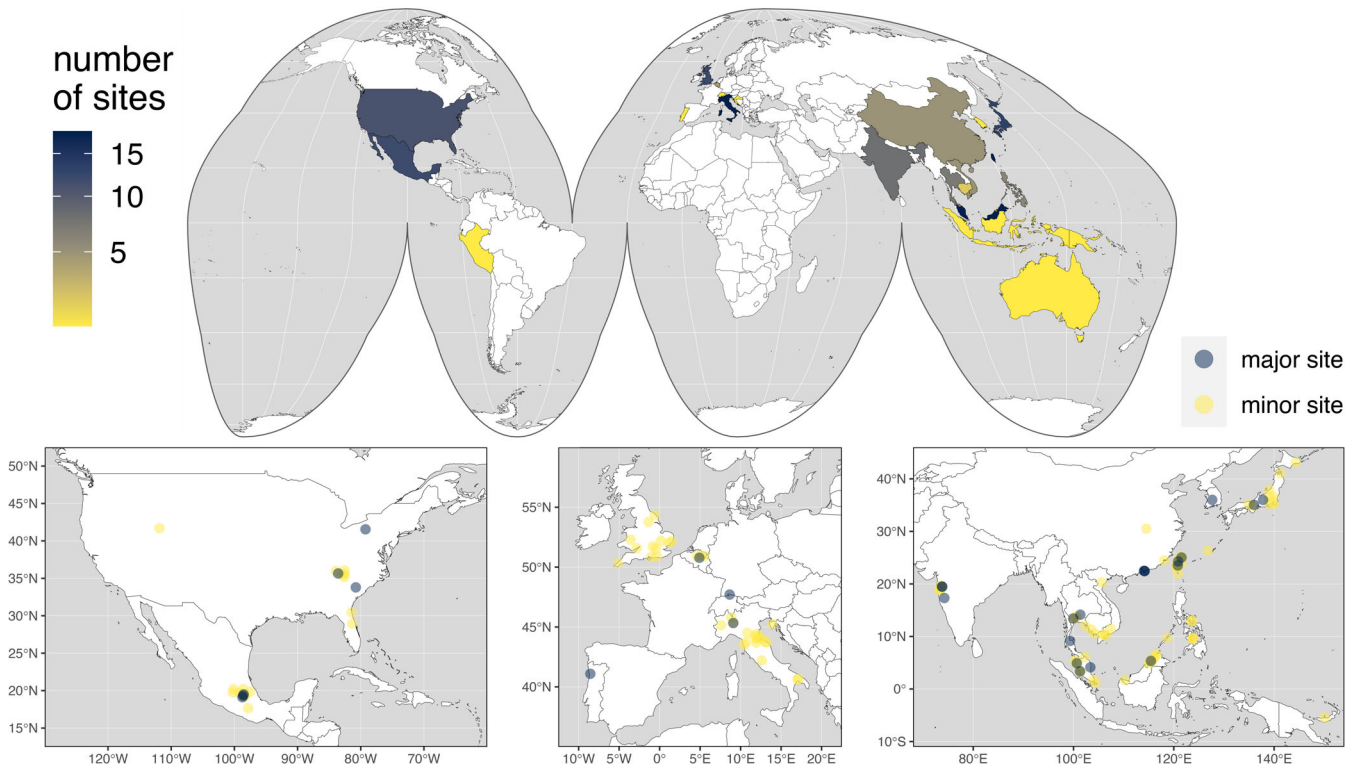

FIGURE 3 Firefly tourism sites around the world. Global map indicates the number of sites reported within various countries (white indicates areas where no firefly tourism sites were reported). Below, maps of North America, Europe, and Asia show locations of the major firefly tourism sites (indicated by blue dots, with details given in Table 2) and additional sites (yellow dots) documented by interviews, online survey and internet searches (see Section 4; site information provided in Table S1)

recreational activity not only in Japan and Thailand, but also in Korea, Taiwan, Malaysia, India, Mexico, and the United States. While knowledge about firefly tourist sites was previously spread by word of mouth, in magazines, or through newspaper articles, the internet has fueled many sites' skyrocketing popularity through websites and photographs available on social media and travel blogs. Like other photogenic experiences that are shared widely (Boley, Jordan, Kline, & Knollenberg, 2018), firefly photography exerts a strong influence on tourists' choices of future travel destinations.

4 | METHODS

This study was initiated in 2018 and included four main components. The first consisted of targeted in-person interviews by phone or by email with informants knowledgeable about well-known firefly tourism products: these include firefly-watching sites in Malaysia, Thailand, Taiwan, USA, Korea, Europe, and Mexico. Informants included scientists, government officials, tour guides, and independent entrepreneurs. The second component consisted of an online survey (Dolnicar, Laesser, & Matus, 2009; Sexton, Miller, & Dietsch, 2011) sent in February 2020 to an additional 20 people involved in firefly tourism around the world whom we contacted through the Fireflyers International Network Facebook group. The survey consisted of 12 questions that solicited information on site locations, firefly species, visitor numbers, trail access, and whether or not tourists were given guidelines concerning appropriate firefly-watching behavior.

The third component was an internet Google search (Gursoy & McCleary, 2004; Vila et al., 2018) to locate firefly tourism sites that either maintained a website, received online reviews, or were mentioned in travel blogs (search terms in English "firefly + tour" and "firefly + ecotour"): although extensive, this search was not intended to be exhaustive. Additional sites were included based on several authors' personal knowledge. These sources were compiled into a global map of firefly tourism sites (Figure 3). For the fourth component of this study, we applied knowledge about firefly ecology and behavior to develop general guidelines that may be adopted by practitioners and tourists in order to better conform with ecotourism standards.

Finally, to illustrate more vividly some on-the-ground challenges and successes inherent in managing firefly tourism, we complement our global overview with in-

TABLE 2 Table of major tourist sites by geographic region and country with firefly species, type, and courtship display season, estimated number of tourists per year, fees, trail type, site protection (none, government, NGO), and tourist guidelines (none, display, announced, handout)

Site name	Location	Focal species	Firefly type	Display season	Estimated # visitors	Fees?	Trail type	Protection	Guidelines
Southeast Asia									
Thailand: Amphawa (Mae Klong River, Samut Songkram Province)[a]	13.425211, 99.954973	*Pteroptyx malaccae, P. valida*	Adults congregating, synchronous; larvae semi-aquatic	Year round	>19,200	Yes	Water (motorboats)	None	None
Thailand: Bang Bai Mai (Tapi River, Surat Thani Province)[a]	9.151032, 99.307135	*Pteroptyx valida, P. malaccae, P. aymmetria, P. tener*	Adults congregating, synchronous; larvae semi-aquatic	Year round	12,000	Yes	Water (motorboats, some rowed)	None	None
Thailand: Phrom Yothi Military Camp (Prachin Buri Province)[a]	14.137641, 101.358429	*Asymmetricata circumdata*	Adults flash; larvae terrestrial	June–august	3,500	No	Road to raised walkway	gov	Display
Malaysia: Kampung Kuantan, Kuala Selangor, (Selangor state)[b]	3.367681, 101.3007151	*Pteroptyx tener, P. malaccae*	Adults congregating, synchronous; larvae semi-aquatic	Year round	>40,000	Yes	Water (rowboats)	gov	Display
Malaysia: Sungai Klias (Sabah state)[b]	5.346571, 115.432248	*Pteroptyx tener, P. malaccae, P. bearni, P. valida*	Adults congregating, synchronous; larvae semi-aquatic	Year round	100,400	Yes	Water (motorboats)	gov	Announce
Malaysia: Sungai Cherating (Pahang state)[c]	4.1264542, 103.3612664	*Pteroptyx bearni*	Adults congregating, flash; larvae semi-aquatic	Year round	15,000	Yes	Water (motorboats)	gov	Display, announce
Malaysia: Sungai Sepetang (Perak state)[d]	4.909063, 100.664759	*Pteroptyx tener, P. malaccae, P. valida*	Adults congregating, synchronous; larvae semi-aquatic	Year round	>8,000	Yes	Water (motorboats)	None– >gov	None
India: Purushwadi, Bhandardara, Rajmachi (Western Ghats, Maharashtra state)[e]	18.4083398, 73.4342518	*Abscondita* sp.	Adults congregating, synchronous; larvae terrestrial	May–June	35,000	Yes	Walking trail	None	
Asia									
South Korea: Muju firefly festival (Muju County, Jeolla Province)[f]	36.002326, 127.662515	*Pyrocoelia rufa*	Adults flash, females flightless; larvae terrestrial	September	200,000	Yes	Walking trail	gov	Display, announce
Japan: Moriyama (Shiga Prefecture)[g]	35.0504109, 135.9956896	*Luciola cruciata*	Adults flash (sometimes synchronous); larvae aquatic	May–June	60,000	No	Walking trail	gov	Display, handout,
Japan: Tatsuno (Nagano Prefecture)[g]	35.9861771, 137.7987524	*Luciola cruciata*	Adults flash (sometimes synchronous); larvae aquatic	June	140,000	Yes	Walking trail	gov	Display, announce

(Continues)

TABLE 2 (Continued)

Site name	Location	Focal species	Firefly type	Display season	Estimated # visitors	Fees?	Trail type	Protection	Guidelines
Taiwan: Alishan National Scenic Area (Chiayi County)[h]	23.509056, 120.802111	*Abscondita cerata*, *A. anceyi*, (spring); *Pyrocoelia praetexta, Diaphanes citrinus* (autumn); *D. nubilis, D. lampyroides* (winter)	Adults flash, larvae terrestrial	March–May, October–November	>346,000	Yes	Forest trail and raised boardwalk	gov	Display, announce
Taiwan: Tungshih Forest Area (Taichung County)[h]	24.285276, 120.867651	*Abscondita cerata*, *A. anceyi*, *Luciola kagiana* (spring), *Pyrocoelia* (autumn)	Adults flash, larvae terrestrial	April–May, October–November	>192,000	Yes	Forest trail, raised boardwalk	gov	Display, announce
Taiwan: Daan Forest Park (Taipei City)[h]	25.033303, 121.535844	*Abscondita cerata*, *Aquatica ficta*	Adults flash, larvae terrestrial (*A.cerata*) or aquatic (*A. ficta*)	April–May	21,000	No	Park trail	gov	Display, announce
Hong Kong: Tai Po Kau Nature Reserve[i]	22.428520, 114.180591	*Pygoluciola qingyu, Pyrocoelia lunata, Diaphanes citrinus*	Adults congregating, adult flash; larvae terrestrial	May–August; Nov–Dec	5,000–10,000	Yes	Concrete road, forest trail	gov	Display
Hong Kong: Mai Po Ramsar site[i]	22.493457, 114.034196	*Pteroptyx maipo*	Adults congregating, adult flash; larvae terrestrial	May–Sept	500–1,000	Yes	Walking trail	NGO	Display, announce
Hong Kong: Sha Lo Tung[i]	22.478840, 114.182683	*Abscondita terminalis*	Adults congregating, adult flash; larvae terrestrial	May–Sept	200–600	Yes	Walking trail	NGO	Display, announce
North America									
USA: Great Smoky Mountains National Park [Elkmont firefly event] (Tennessee)[j]	35.652882, −83.577263	*Photinus carolinus*	Adults synchronous; larvae terrestrial	Late May–early June	26,000 [>12,000]	Yes[k]	Shuttle bus, forest trail	Gov	Handout
USA: Congaree National Park (Hopkins, South Carolina)[l]	33.7948001, −80.7820962	*Photuris frontalis*	Adults synchronous; larvae terrestrial	May	12,500	No	Forest trail (one-way), raised boardwalk	Gov	Website
USA: Pennsylvania Firefly Festival (Tionesta, Pennsylvania)[m]	41.5509267, −79.2508314	*Photinus carolinus*	Adults synchronous; larvae terrestrial	June	1,000	Yes	Forest trail	None	Handout, announce
Mexico: Nanacamilpa (~24 sites) (State of Tlaxcala)[n]	19.493015, −98.535927	*Photinus palaciosi*	Adults synchronous, females flightless; larvae terrestrial	June–August	120,000	Yes	Forest trail	Varies	Display, announce (some sites)

TABLE 2 (Continued)

Site name	Location	Focal species	Firefly type	Display season	Estimated # visitors	Fees?	Trail type	Protection	Guidelines
Mexico: Santa Rita Tlahuapan (State of Puebla)[n]	19.323566, −98.615653	*Photinus palaciosi*	Adults synchronous, females flightless; larvae terrestrial	June–August	1900	Yes	Forest trail	Gov	Display, announce
Mexico: Bosque Esmeralda (State of México)[n]	19.12436, −98.72842	*Photinus palaciosi*	Adults synchronous, females flightless; larvae terrestrial	June–August	7,850 (2019)	Yes	Forest trail	n/a	Display, announce
Europe									
Belgium: Rommersom, Hoegaarden[o]	50.7807906, 4.9125614	*Lamprohiza splendidula, Lampyris noctiluca*	Adults glow, females flightless; larvae terrestrial	June	50–100	No	Walking trail	NGO	Display, handouts
Portugal: Parque Biológico de Gaia, Avintes[o]	41.097304, −8.554185	*Luciola lusitanica*	Adults flash; females flightless; larvae terrestrial	June	1,000–2000	Yes	Walking trail	Gov	Announce
Switzerland: Waldfriedhof, Schaffhausen[p]	47.707954 1,8.6494835	*Lamprohiza splendidula*	Adult glow, females flightless; larvae terrestrial	June	2000	No	Walking trail	Gov	Display, announce
Italy: Bosco Bria, Binasco (Lombardy)[q]	45.3333757, 9.0961218	*Luciola italica*	Adults flash; females flightless; larvae terrestrial	June	500	No	Walking trail	Gov	Announce

Note: Citations/references in footnotes.

[a]Dr. Anchana Thancharoen, Kasetsart University, pers. comm.

[b]C.H. Wong, Malaysian Nature Society, pers. comm., # visitors at Kampung Kuantan in 2010 from Shahwahid, Iqbal, Ayu, & Farah, 2013, # visitors at Selangor Klias in 2017 from Dr. F.H. Binti Saikim and Elora Poukin, pers. comm.

[c]Ohba & Wong, 2012, Mohd Hafiz, Hafiz Cherating Tours, pers. comm.

[d]Jusoh et al. 2018, pers. comm.

[e]Dr. Hemant Ghent, Dr. Krushnamegh Kunte and Mitali Inamdar, pers. comm.

[f]Hwang, Moon, Lee, Kim, & Kim, 2020 and Dr. Shin-il Jo, Seoul Zoo, pers. comm.

[g]Hosaka, Kurimoto, & Numata, 2016 and Dr. Yuichi Oba, Chubu University, pers. comm.

[h]Dr. Chiahsiung Wu, Huafan University, pers. comm.

[i]Vor Yiu, Hong Kong Entomological Society, pers. comm.

[j]Dana Soehn and Becky Nichols, GSMNP, pers. comm.

[k]Parking fee only.

[l]Dr. David Shelley, Congaree NP pers. comm. and website https://www.nps.gov/cong/fireflies.htm.

[m]Peggy Butler, PA Firefly Festival, pers. comm.

[n]Dr. Paola Velasco Santos and Tania López-Palafox, UNAM, pers. comm.

[o]De Cock, Alves, Oliveira, & Gomes, 2015, Dr. Raphael De Cock, University of Antwerp, pers. comm.

[p]Stefan Ineichen, Verein Glühwürmchen Projekt, pers. comm.

[q]Dr. Giuseppe Camerini, Lucciole d'Italia (Coleoptera Lampyridae), pers. comm.

depth case studies gathered from different geographical regions (below and Appendix S1—Conservation Stories).

5 | RESULTS: FIREFLY TOURISM AROUND THE WORLD

Targeted interviews and an online survey revealed that firefly tourism is highly popular across a broad geographic scope, as destinations in 12 countries collectively attract over one million visitors annually (Table 2). Currently, the most-visited tourist sites are located in Asia. For example, in Korea in 2019 more than 200,000 visitors attended the annual 9-day Muju Firefly Festival to watch *Pyrocoelia rufa* fireflies, among other activities. In Taiwan, the government proclaimed 2002 as the Year of Ecotourism and began actively promoting more than 30 firefly sites around the country (Taiwan Tourism Bureau, 2017), turning firefly-watching into a popular recreational activity. Several sites in Taiwan's Alishan National Scenic Area now collectively attract 346,000 visitors to view various species whose courtship displays occur during spring, autumn, or winter (Table 2; case study described in Appendix S1). In Japan, many towns host annual firefly festivals (known as *hotaru matsuri*) that attract thousands of tourists from all over the country (Haugan, 2019; Hosaka et al., 2016). In Hong Kong firefly tourism is concentrated at the Tai Po Kau Nature Reserve, where an estimated 5,000–10,000 visitors arrive during July and August to see *Pygoluciola qingyu* (adults) and *Pyrocoelia lunata* (larvae).

In Southeast Asia, the most popular sites feature congregating fireflies in the genus *Pteroptyx*, which visitors watch from boat tours along mangrove rivers (Table 2 and Figure 2a). The top sites in Thailand (Mae Klong River in Amphawa; case study described below) and Malaysia (Sungai Klias in Sabah) annually draw more than 19,200 and 100,400 tourists, respectively. Certain terrestrial firefly species are also gaining popularity, such as *Asymmetricata circumdata* at a military base in Prachin Buri Province, Thailand. In India rural villages including Purushwadi and Bhandardara in the Western Ghats, Maharashtra State have recently become popular destinations to see terrestrial *Abscondita* sp. fireflies, attracting an estimated 35,000 tourists during their May–June breeding season.

In North America, the number of people traveling to see fireflies has grown dramatically during the past decade. Until the mid-1990s the synchronous flash displays of *Photinus carolinus* in Elkmont, Tennessee (USA) were known only to local residents (Faust, 2017), but now over 12,000 visitors each year travel to the Great Smoky Mountains National Park to attend an 8-day firefly-watching event (Table 2 and Figure 2c; case study described in Appendix S1). Similarly, since 2014 the Congaree National Park in South Carolina has become an increasingly popular place to see another synchronous firefly, *Photuris frontalis*; in May 2019, 12,500 visitors attended what has been expanded into an 18-day event there (www.nps.gov/cong/fireflies.htm). On forested slopes of the Eje Volcánico Transversal in Central Mexico, *Photinus palaciosi* is a synchronous firefly that occurs in scattered populations across the states of Tlaxcala, Puebla, and Estado de México. Since this species was first described in 2012, firefly tourism in Mexico has skyrocketed in popularity (Lemelin, Jaramillo-López, López-Ocaña, & Del-Val, 2020); the best-known municipality of Nanacamilpa (population 15,000) received an estimated 120,000 tourists who visited ~24 sites during the June–August 2019 firefly mating season (Table 2 and Figure 2b). Such popularity has encouraged a rapid proliferation of firefly tourist operations, with over 50 sites currently located across six Mexican states (case study described in Appendix S1).

Europe also has firefly tourism that draws visitors beyond local residents, although this takes place on a considerably smaller scale and often consists of free events hosted by volunteers representing local conservation organizations (Table 2). For 20 years, Parque Biológico de Gaia in Portugal has hosted a June firefly event that attracts more than 1,000 visitors over a 2-week span (De Cock et al., 2015). In many parts of Italy, nature associations advertise "magic nights" during June where the public can enjoy watching two flashing species, *Luciola lusitanica* and *L. italica*, in their natural habitat. For example in the town of Binasco near Milan, guided tours hosted each June by local volunteers bring 500 visitors to Bosco Bria to see *L. italica* (Camerini, 2008). In Belgium, similar nature organizations guide ~50–100 people at local sites to see the glow-worm fireflies *Lamprohiza splendidula* and *Lampyris noctiluca*. Such excursions have boosted public support for nature organizations as well as participation in firefly citizen-science projects (De Cock, pers. observation).

Seasonality of firefly tourism depends both on geographic location and on species ecology (Table 2). In Southeast Asia, adults of various *Pteroptyx* spp. actively display and attract visitors year-round. In India, however, firefly tourism is restricted to several weeks during late May to early July when *Abscondita* sp. fireflies produce their mating displays. Firefly tourism in Europe and North America is also highly seasonal, as it is concentrated within the short breeding season of each species, which may last only a few weeks (*Photinus carolinus*, *Photuris frontalis*) or months (*Photinus palaciosi*).

Many firefly species prominently featured at popular sites possess life history traits and behaviors that make them especially vulnerable to tourism-associated threats. Species that produce synchronous courtship displays (in which many adult males flash on and off in unison) appear to be

especially popular attractions (Table 2). In Thailand and Malaysia this includes *Pteroptyx* spp. that form highly localized breeding congregations in certain trees along mangrove rivers; their habitat specificity and site fidelity make them particularly susceptible to habitat loss, degradation and light pollution from tourism-associated infrastructure and tourist activity. The most popular tourist sites in North America also showcase synchronous species (i.e., *Photinus palaciosi*, *Photinus carolinus*, and *Photuris frontalis*). Although their breeding aggregations tend to be more dispersed, these latter species have brief mating seasons that temporally constrain the tourist season into a few weeks or months, increasing the potential for visitation rates to exceed carrying capacity and to disrupt firefly reproduction. Some sites feature firefly species whose females are flightless and therefore particularly vulnerable to trampling, such as *Photinus palaciosi* (Mexico) and *Phausis reticulata* (USA). In Europe, all species at popular tourist sites have flightless females, including *Lamprohiza splendidula*, *Lampyris* spp. *Luciola lusitanica*, and *L. italica*.

Depending on the location, tourists gain access to firefly display sites using various types of trails (Table 2). Because *Pteroptyx* and other congregating mangrove fireflies display on visually prominent trees located along tidal rivers (Jaikla, Lewis, Thancharoen, & Pinkaew, 2020), these sites are mainly accessed by boat. At some of these sites (e.g., Amphawa, Thailand) tour guides use motorboats, while at others (e.g., Kampung Kuantan, Selangor, Malaysia) tourists are rowed along the river in traditional sampans (Figure 2a). High-speed motorboat traffic associated with firefly tours has been observed to cause riverbank erosion and water pollution (Thancharoen, 2012). At other sites, tourists gain access to the firefly display by following foot trails through the forest or grassland habitat. Heavy foot traffic has the potential to degrade habitats for fireflies and their prey, and to directly harm their terrestrial juvenile stages (eggs, larvae, pupae), as well as flightless females and mating pairs. During firefly tours at Parque Biológico de Gaia in Portugal visitors are guided in small groups that are strictly limited to existing paths to reduce habitat disturbance. Some sites in Taiwan, Japan, and Thailand have constructed raised boardwalks and viewing platforms to protect adult display areas and larval habitat. In the USA, Congaree National Park restricts visitors to a one-way forest trail whose edges are cordoned off to protect firefly habitat. To reduce visitors' flashlight use, trail edges are illuminated with low-intensity red lights, and a raised boardwalk is also available at this site for visitors with limited mobility.

While many tourist sites are located in protected areas owned by either government organizations or NGOs (Table 2), only a handful have been specifically designated to protect firefly habitat. Beginning in 1924, the Japanese government established several Natural Monuments that provide legal protection for the habitat of the Genji firefly *Luciola cruciata* (Lewis, 2017), whose aquatic larvae and their snail prey inhabit clean, fast-flowing rivers; indeed, tourism and firefly habitat protection have been closely intertwined in Japan for decades (Haugan, 2019; Lewis, 2016). In Korea's Muju County three firefly species (*Pyrocoelia rufa*, *Luciola lateralis*, and *Hotaria unmunsana*) together with their habitats and prey have enjoyed protection since 1982, when they were designated as Korean Natural Monument No. 322. In Taiwan two species, *Aquatica hydrophila* and *Pristolycus kanoi*, are designated as rare and valuable under a national Wildlife Conservation Act, which also protects portions of their mountain stream and waterfall habitats. At Kampung Kuantan in Malaysia, *Pteroptyx* fireflies and their habitat are protected by the government under Selangor Water Management Board (LUAS) Enactment 1999 (Khoo, Nada, Kirton, & Phon, 2012; Wong & Yeap, 2012).

In addition to the major sites described in Table 2, many additional firefly tourism sites were revealed by our informant interviews, online survey and internet search of websites, reviews, and travel blogs (designated as "minor" sites in Figure 3 and Table S1). These include sites in India, Thailand, Malaysia, Philippines, Vietnam, Cambodia, Japan, Taiwan, Italy, Croatia, Mexico, United States, United Kingdom, and China. Although included in Figure 3, sites in the latter two regions are markedly different from other firefly sites described here. In the United Kingdom, many nature organizations sponsor annual glow-worm excursions that typically attract only a few dozen local people; as they neither travel from afar nor require food and lodging, such participants might not even be considered tourists (Robin Scagell, UK Glow-worm Survey, personal communication). In China, firefly viewing events typically have been held in large theme parks where many thousands of wild-harvested insects are released into an artificial environment. Such exhibitions pose entirely different threats because they depend on large-scale harvesting of firefly adults from wild populations, and because fireflies removed from their natural habitat are unlikely to successfully reproduce (Lewis & Owens, 2017). Recently, however, progress has been made toward designating and protecting some natural habitats for firefly tourism in China (Dr. Xinhua Fu, Huazhong Agriculture University, personal communication).

6 | CASE STUDY OF AMPHAWA, THAILAND

Although every firefly tourism site depends on an identical resource—the bioluminescent courtship display of adult fireflies—each has a unique combination of adult and larval habitat requirements, local governance, economic factors, cultural, and historical settings. To illustrate some on-the-ground challenges and successes inherent in managing

firefly tourism, we present here a case study tracing a precipitous 20-year decline in firefly tourism in Amphawa, Thailand. Additional case studies from USA, Mexico, and Taiwan are included as Conservation Stories in online Appendix S1. Because each case is based on decades of personal experience by one of our co-authors, we have chosen to share these in narrative format.

In Thailand, fireflies are considered economic insects, based on the potential for firefly tourism to benefit local people, businesses and government organizations. In recent years, one of the most popular firefly sites in Thailand has been the village of Amphawa, located approximately 90 km southwest of Bangkok in Samut Songkhram Province (Thancharoen, 2012). Canals connect the village to the mangrove-lined Mae Klong River, once home to dazzling numbers of *Pteroptyx malaccae* fireflies. In this and other *Pteroptyx* species, their entire life cycle takes place within riparian zones of tropical mangrove forests (Loomboot, 2008). Adult males congregate in visually prominent display trees (most often *Sonneratia caseolaris*) and emit synchronous courtship flashes. Females are attracted to this display and fly to the trees, mate, then lay their eggs in nearby soil and leaf litter. Eggs usually hatch within 12 days, and larvae hunt mangrove and freshwater snails as they continue to grow for about 3 months. Once they are fully grown, the larvae pupate in soil near plant roots above the high tide zone, emerging about 10 days later as adults and returning to the display tree.

In 2004, the district government initiated a tourism development plan for Amphawa. They promoted nighttime boat cruises to visit the firefly trees, which they coupled with a revived afternoon floating market held along the canal. In the beginning, there were numerous firefly display trees along the Mae Klong River, and tourists came from all over Thailand and beyond to watch the displays. The number of tour operations grew rapidly, increasing from seven tour boats in 2004 to 180 in 2010. By 2006, Amphawa had become the top firefly tourism destination in Thailand. Unfortunately, no limits were set on the numbers of boats, visitors, or tours per night, and no guidelines were implemented to protect the local firefly population.

Commercial development was not well-regulated, and the construction of many new resorts and restaurants along the river disturbed the riparian mangrove zone, removing firefly display trees and destroying larval habitats. As the economy shifted from agriculture to tourism, local residents did not necessarily benefit: some tourism-related businesses were run by locals, but many others were heavily capitalized by tour operators from outside the community (Thancharoen, 2012). Conflict arose between tour operators and local residents. By 2006, although a few tours used rowboats, most tour operators were using larger motorboats holding up to 30 customers and propelled by powerful 320 hp diesel engines. At peak times, there could be more than 200 motorboat trips per night, often continuing past midnight. People living along the riverbanks complained about late-night disruption from noisy tour boats, and one resident even cut down a firefly display tree to halt this nightly disturbance. Local residents set up buoys to protect firefly areas, which were sometimes removed by tour guides trying to get customers closer to the display trees.

Unregulated tourism had many adverse effects on the firefly population near Amphawa. Bright lights from the new resorts shone out onto the river. Additional artificial illumination from boats lights, flashlights and camera flashes disturbed firefly courtship behavior. Tour guides sometimes bumped their boats against display trees so tourists could watch the insects take flight. Heavy motorboat traffic contaminated the river with motor oil and generated waves that caused riverbank erosion, toppling preferred firefly display trees into the river. This constant wave action also washed away the mud along the riverbanks, habitat essential for larval fireflies and their snail prey. The cumulative effects of these tourism-related activities have reduced the local population of *Pteroptyx malaccae* in Amphawa by an estimated 80% (A. Thancharoen, unpublished data). Visitors now come to Amphawa mainly to see the afternoon floating market and to take daytime river cruises.

P. malaccae remains widely distributed in other parts of Thailand (Jaikla et al., 2020), and the lessons learned from Amphawa's failure will be useful in developing other firefly tourism sites. To encourage more sustainable tourism at Amphawa and other sites, researchers at Kasetsart University have designed and installed interpretive displays and brochures describing firefly life cycles, behavior, and species conservation. They have also run voluntary training programs for tour operators, tourboat guides, local residents and school children. Such programs have raised awareness among diverse stakeholders about ways to benefit local communities while increasing protection for the fireflies and their habitat (Nurancha, Inkapatanakul, & Chunkao, 2013).

7 | MOVING TOWARDS SUSTAINABLE FIREFLY ECOTOURISM

In this section, we offer guidelines intended to support practitioners interested in moving towards firefly ecotourism, consistent with Fennell's definition as a "sustainable, non-invasive form of nature-based tourism that focuses primarily on learning about nature first-hand,

and which is ethically managed to be low impact, non-consumptive, and locally oriented (control, benefits, and scale)" (Fennell, 2008, p. 24).

Although the study of ecotourism has been critiqued for its normative approach (e.g., Thompson, Gillen, & Friess, 2018), our goal is to provide a flexible set of guidelines that can be adapted to fit local circumstances. Because every firefly tourist site represents a unique set of biological, social, and economic factors, no guidelines will be universally applicable. Yet we contend that every site can develop a management plan that works to protect fireflies by conserving the habitats required by all life stages, to involve local communities as key stakeholders, and to provide training programs for guides and interpretive exhibits for visitors. Below we suggest science-based best practices for firefly tour operations, followed by suggestions for tourist behaviors that will minimize impacts on firefly populations (firefly-watching etiquette).

7.1 | Best practices for firefly tour operations

To help protect firefly populations and enhance the visitor experience, we recommend that private and public tour operators at firefly sites take the following actions:

7.1.1 | Conserve the habitats required for all life stages to thrive

Tourist sites must protect not only the habitats where adult courtship occurs, but also the habitats occupied by fireflies' juvenile life stages and their larval prey (e.g., forests, wetlands, grasslands for species with terrestrial larvae, rivers and ponds for those with aquatic larval stages, riverbank mangrove forests for congregating mangrove fireflies). To accomplish this, it may be necessary to rope off viewing areas to restrict visitors to designated zones or trails, to build raised walkways and viewing platforms, or to set limits on visitor carrying capacity. When tourists access sites by water, tours should use non-motorized or electric boats, and no-wake zones should be established and enforced to prevent riverbank erosion. Whether firefly tourism sites are located on public or private land, we advocate formally establishing firefly sanctuaries where management practices can be implemented to preserve the conditions necessary for fireflies to thrive. This includes minimizing use of broad-spectrum insecticides, which have been shown to cause mortality of adult and juvenile fireflies and their prey (reviewed by Lewis et al., 2020). Light pollution is known to disrupt firefly courtship (reviewed by Owens & Lewis, 2018), so artificial lighting within firefly sanctuaries (including streetlights, car headlights, and lighting fixtures around buildings and restroom facilities) should be kept to a minimum while still maintaining visitor safety.

Monitoring programs can be set up to measure conservation outcomes by tracking trends in wildlife abundance at heavily trafficked tourist destinations compared with nearby sites lacking tourists (Durham, 2008; Stronza et al., 2019; Wardle et al., 2018). In 2020, the COVID-19 pandemic provided a natural (though unreplicated experiment), as most tourist sites remained closed; anecdotal evidence from sites in Mexico and elsewhere suggested that firefly activity increased in the absence of tourists during the breeding season (López-Palafox, personal observation). Engaging tourists as citizen-scientists helping to monitor firefly populations would be beneficial, as such programs can deepen tourists' commitment to fireflies and to biodiversity conservation more broadly (Johansen & Auger, 2013a).

7.1.2 | Involve local communities as key stakeholders

Economic benefits for local communities are necessary but not sufficient to ensure conservation. In addition to providing jobs and revenue, community-based tourism—where local voices, values and knowledge are included in tourism development and management—can promote stewardship and strengthen local institutions for managing natural resources (Salazar, 2012; Stronza et al., 2019; Stronza & Durham, 2008). Community-based conservation is enhanced when residents and local organizations are actively engaged in tourism planning and management (D'Souza et al., 2019; Honey, 2008; Salerno et al., 2021).

In practice, however, integrating local entrepreneurship and environmental stewardship can be a complex undertaking (Thompson et al., 2018). As one example of successful community-based tourism, the Malaysian Nature Society (MNS) has worked for decades with local villages to develop locally based tours of the courtship displays of congregating *Pteroptyx* fireflies that are found along mangrove rivers throughout Southeast Asia (Shahwahid et al., 2013; Wong, 2009). For many years, just a few villagers and fishermen earned supplementary income from conducting boat tours of local firefly displays. In the 1970s, MNS started the first community-based firefly tourism in Kampung Kuantan, Selangor State to benefit a wider group of villagers, who now rotate turns taking visitors along the Selangor River in hand-rowed traditional boats (Figure 2a). MNS has provided training for these guides about firefly life cycles and the need to conserve the mangrove habitat, as well as guidelines for responsible firefly-watching. Similar

community-based tourism has been disseminated to other villages, and there are now over 20 firefly-watching sites around Malaysia. Over the past decade, MNS has created a network of firefly nature guides and boatmen who are quite knowledgeable about firefly behavior, ecology and conservation. This *Firefly Komuniti* gathers yearly to exchange information, share ideas on responsible firefly-watching, and engage in collective problem solving. Although the process is slow and dependent on interest and leadership within local communities, these programs have resulted in diversified livelihoods, revenues for local communities, and habitat rehabilitation at several firefly sites in Malaysia.

7.1.3 | Provide training programs for guides and interpretive materials for visitors

Firefly ecotourism should leverage opportunities to raise awareness about firefly life cycles and habitat requirements, and to promote conservation values more generally. Within host communities, we advocate establishing training programs for tour guides, boat operators, and other community members (e.g., Jeong, Roh, & Yhang, 2005; Thancharoen, 2012). Further, we contend that tourists who experience such a remarkable natural phenomenon should also emerge with an enhanced appreciation for wildlife conservation. Therefore, all tourists should be accompanied by trained guides who can present information and answer basic questions about species' biology, habitat requirements, and conservation issues (Lemelin & Jaramillo-López, 2019; Shahwahid et al., 2013). In addition, ecotourist sites should provide well-designed, accurate interpretive signage and attractive exhibits that enhance such knowledge and promote positive attitudes toward biodiversity conservation (Figures 2d, S1; Thancharoen, 2012).

Although tourism economics lies beyond the scope of the present study, here we briefly address the question of how to pay for these recommended training programs, exhibits, site improvements and habitat protection. From a global economic perspective, it has been estimated that tourism revenues derived from parks and protected areas already far exceed what governments spend on their maintenance, suggesting a capacity for increased investment in maintaining these natural areas (Balmford et al., 2015). Meanwhile, innovative new options for conservation financing are being developed (Epler Wood, Milstein, & Ahamed-Broadhurst, 2019), including public–private partnerships that can help cover the social, cultural and environmental costs of tourism growth.

On public lands tourist fees can be instituted to help cover such costs, but proceeds should remain at the local tourist destination, for example, that particular national park (Watson & Borrie, 2003), and be specifically designated for management, site maintenance and protection of fireflies and their habitats. Private businesses at firefly tourist sites might also allocate a portion of their revenues into a local sustainable tourism fund (e.g., STAMP, Epler Wood, 2017) to help cover costs of infrastructure maintenance as well as natural resource protection. People often experience a powerful emotional connection to the natural world while firefly-watching, thus these insects have the potential to inspire substantial philanthropic donations from tourists to support conservation efforts.

7.2 | Firefly-watching etiquette

We recommend implementing the following guidelines for transforming tourist behavior to help minimize visitor impact on firefly populations and enhance the quality of the firefly experience for all visitors. This section also provides a brief summary of the scientific basis for these guidelines.

- No artificial lights (no flashlights, lanterns, phones, light-up shoes)
- No flash photography
- Stay on the marked trail at all times
- Speak quietly
- Do not capture fireflies or disturb their display sites
- No smoking or heavy perfume
- Cover up for mosquito protection (if you need insect repellent, apply it before arriving at the site)

Various firefly life stages are susceptible to physical disturbance such as handling and trampling, and mating pairs often perch on low vegetation (Faust, 2017; Lewis, 2016; Lloyd, 2008), so tourists should be discouraged from walking through firefly habitat. Bright artificial light is known to obscure or inhibit bioluminescent signals in several firefly species, thereby reducing their courtship success (reviewed by Lewis et al., 2020; Owens & Lewis, 2018; Owens et al., 2020; Owens & Lewis, 2021; Thancharoen & Masoh, 2019). Although many insects are less sensitive to red or amber light (Briscoe & Chittka, 2001; Owens, Meyer-Rochow, & Yang, 2018), differences among firefly species in their range of spectral sensitivity indicates that—regardless of color—artificial illumination at tourist sites should be as dim as possible and used only when necessary for visitor safety. Some fireflies rely on volatile chemicals for courtship (De Cock, Faust, & Lewis, 2014; De Cock &

Matthysen, 2005; Lloyd, 1972; Ohba, 2004), thus smoking or use of strong perfumes should be avoided as this could interfere with perception of these olfactory cues. On-site spraying of DEET and picaridin should be avoided as they have been shown to interfere with insect olfactory receptors and oviposition in other insects (Pellegrino, Steinbach, Stensmyr, Hansson, & Vosshall, 2011; Xu, Zeng, Bedoukian, & Leal, 2019), although we know of no studies that have looked specifically at how various insect repellents affect fireflies. Finally, contact between fireflies and permethrin-impregnated clothing (e.g., BuzzOff®, Insect Shield®) should be avoided because this neurotoxin causes fatal paralysis in insects (Diaz, 2016).

Whenever possible, tourists should be informed about behavioral expectations in advance, for example, on tour websites, via WhatsApp or with email confirmations. In addition, these guidelines should be prominently displayed at the site entrance, should be explained in written, audio, or video formats during tour orientations, and should be strictly enforced by tour guides.

8 | CONCLUSIONS

Fireflies are highly charismatic insects that have recently garnered widespread attention from nature tourists. In this comprehensive review we document the popularity and geographic scope of firefly tourism, revealing that each year over 1 million tourists travel to destinations in at least 12 countries to enjoy this unique wildlife experience. The rapid growth of this industry brings some urgency to the task of devising, distributing, and implementing practices that can help foster the transition from tourism toward ecotourism. Using existing knowledge concerning firefly ecology and behavior, we provide science-based recommendations for how to minimize threats and promote population persistence. In addition, we offer case studies from different geographical regions to more vividly illustrate some real-world challenges and highlight strategies that have been successful in benefitting local communities while also protecting firefly populations.

A fundamental tenet of ecotourism is conserving the value of the natural resource at tourist destinations. Importantly, developing an effective management plan for firefly tourism requires protecting not only the habitats that adult fireflies use for their bioluminescent courtship displays, but also those habitats essential for female oviposition, larval growth and development, and pupation. Acknowledging the scope of firefly tourism and its contribution to local and national economies could help motivate the establishment of legally protected firefly sanctuaries. For example, congregating fireflies such as *Pteroptyx* spp., which rely on the mangrove ecosystem for completion of their life cycle, represent a potential flagship species for conservation of riparian mangrove forest. Although flagship species most typically consist of charismatic megafauna, *Pteroptyx* fireflies could stimulate establishment of Key Biodiversity Areas (IUCN, 2016) that may simultaneously help protect multiple taxonomic groups. For example, protecting habitat required by adult and larval *Pteroptyx* fireflies could aid conservation efforts for the milky stork (*Mycteria cinereal*), silvery langur (*Trachypithecus cristatus*), dugong (*Dugong dugon*), reticulated python (*Malayopython reticulatus*), and several terrapins within Southeast Asian mangrove forests (Thompson & Rog, 2019).

While firefly ecotourism has the potential to yield substantial economic benefits across multiple scales ranging from local communities, states, regions, and nations, some investment is necessary to ensure long-term survival and reproduction of the focal firefly species. As emphasized by Thompson et al. (2018), no one-size-fits-all solution exists because ecotourism is embedded in so many different biological, cultural, political, and socioeconomic contexts. In addition to the best practices we have outlined here, our broad recommendations include reserving some portion of tourist revenues to be managed and used locally for site maintenance, interpretive exhibits, and firefly habitat protection. National tourism agencies might sponsor training programs for local guides, working in collaboration with academic institutions, NGOs, and conservation groups. Local communities need to be actively engaged in tourism planning and management, with logistical and financial support made available to strengthen local institutions that are ultimately responsible for on-the-ground conservation management.

Moving forward, our IUCN SSC Firefly Specialist Group is prepared to assist stakeholders at firefly tourist sites with their conservation planning efforts. Additional work is underway to provide resources accessible to the general public concerning firefly ecology and conservation, such as De Cock et al. (2015) and Fallon et al. (2019), as well as publications specifically designed for firefly tourists, such as the highly informative guide *Firefly-Watching in Taiwan* (Taiwan Tourism Bureau, 2017). In addition to working to conserve firefly populations, we remain optimistic about the possibility of leveraging fireflies' widespread popularity to raise public awareness and spark enthusiasm for invertebrate conservation more generally.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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REFERENCES

Allen, L., & Wilson, J. (Eds.). (1992). *Lafcadio Hearn: Japan's great interpreter. A new anthology of his writings 1894–1904*. Sandgate, UK: Japan Library Ltd.

Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., ... Manica, A. (2015). Walk on the wild side: Estimating the global magnitude of visits to protected areas. *PLoS Biology*, *13*(2) Retrieved from, e1002074. https://doi.org/10.1371/journal.pbio.1002074

Bilkovic, D., M. Mitchell, J. Davis, E. Andrews, A. King, P. Mason, J. Herman, N. Tahvildari, J. Davis (2017). Review of boat wake wave impacts on shoreline erosion and potential solutions for the Chesapeake Bay. STAC publication number 17–002, Edgewater, MD. 68 pp. doi:https://doi.org/10.25773/v5-qsqm-kf90

Boley, B. B., Jordan, E. J., Kline, C., & Knollenberg, W. (2018). Social return and intent to travel. *Tourism Management*, *64*, 119–128.

Borges, M.A., R. Bushell, G. Carbone, and T. Jaeger (2011). *Sustainable tourism and natural world heritage: Priorities for action*. Gland, Switzerland: International Union for the Conservation of Nature. Retrieved from https://portals.iucn.org/library/node/9789

Branham, M. A., & Wenzel, J. (2003). The origin of photic behavior and the evolution of sexual communication in fireflies. *Cladistics*, *19*, 1–22.

Briscoe, A. D., & Chittka, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology*, *46*, 471–510. https://doi.org/10.1146/annurev.ento.46.1.471

Buckley, R. (2009). *Ecotourism: Principles and practices*. Cambridge, MA: CAB International.

Buckley, R., & Pannell, J. (1990). Environmental impacts of tourism and recreation in national parks and conservation reserves. *Journal of Tourism Studies*, *1*, 24–32.

Buckley, R., Brough, P., Hague, L., Chauvenet, A., Fleming, C., Roche, E., ... Harris, N. (2019). Economic value of protected areas via visitor mental health. *Nature Communications*, *10*, 5005.

Camerini, G. (2008). *A biotope for fireflies. Ecosoft art, a park in movement* (pp. 81–83). Turin: Parco Arte Vivente.

Ceballos-Lascurain, H. (1996). *Tourism, ecotourism and protected areas*. Gland, Switzerland: IUCN, The World Conservation Union.

Ceballos-Lascurain, H. (2012). Retos, Avances y Tendencias del Turismo de Naturaleza y Ecoturismo en Asia del Este y América Latina. Paper presented at the Presentation at 3rd International Conference FEALAC on Nature Tourism and Ecotourism, Barranquilla, Colombia.

De Cock, R., & Matthysen, E. (2005). Sexual communication by pheromones in a firefly, *Phosphaenus hemipterus* (Coleoptera: Lampyridae). *Animal Behaviour*, *70*, 807–818.

De Cock, R., Faust, L., & Lewis, S. M. (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.

De Cock, R, H. N. Alves, N. G. Oliveira and J. Gomes (2015). *Fireflies and Glow-worms of Portugal* [In Portuguese and English]. Águas e Parque Bioológico de Gaia, EEM/Câmara Municipal de Vila Nova de Gaia. 80 pp.

Diaz, J. H. (2016). Chemical and plant-based insect repellents: Efficacy, safety, and toxicity. *Wilderness and Environmental Medicine*, *27*, 153–163. https://doi.org/10.1016/j.wem.2015.11.007

Dolnicar, S., Laesser, C., & Matus, K. (2009). Online versus paper: Format effects in tourism surveys. *Journal of Travel Research*, *47*, 295–316. https://doi.org/10.1177/004728750 8326506

D'Souza, C., Taghian, M., Marjoribanks, T., Sullivan-Mort, G., Manirujjaman, M. D., & Singaraju, S. (2019). Sustainability for ecotourism: Work identity and role of community capacity building. *Tourism Recreation Research*, *44*, 533–549.

Durham, W. H. (2008). The challenge ahead: Reversing vicious cycles through ecotourism. In A. L. Stronza & W. H. Durham (Eds.), *Ecotourism and conservation in the Americas, Ecotourism Series No. 7* (pp. 265–271). Cambridge, MA: CAB International.

Durkheim, E. (1912). *The elementary forms of religious life. Paris, F. Alcan. Translated by KE Fields* (p. 1995). New York: Simon & Shuster.

Epler Wood, M. (2017). *Sustainable tourism on a finite planet*. Oxon, UK: Routledge.

Epler Wood, M., Milstein, M., & Ahamed-Broadhurst, K. (2019). *Destinations at risk: The invisible burden of tourism*. Ithaca, NY: Centre for Sustainable Global Enterprise and EplerWood International, Cornell University.

Fallon, C., Hoyle, S., Lewis, S., Owens, A., Lee-Mader, E., Black, S. H., & Jepsen, S. (2019). *Conserving the jewels of the night: Guidelines for protecting fireflies in the United States and Canada* (p. 48). Portland, OR, USA: The Xerces Society for Invertebrate Conservation. https://xerces.org/sites/default/files/publications/19-049_01_Firefly%20guidelines_web_1.pdf

Faust, L. F. (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. https://doi.org/10.1653/024.093.0210

Faust, L. F. (2017). *Fireflies, Glow-worms, and lightning bugs: Identification and natural history of the fireflies of the eastern and Central United States and Canada* (p. 376). Athens, Georgia: University of Georgia Press.

Fennell, D. A. (2008). *Ecotourism* (3rd ed.). Routledge: London.

Fennell, D. A. (2020). *Ecotourism* (5rd ed.). Routledge: London.

Fu, X., Ballantyne, L., & Lambkin, C. (2012). The external larval morphology of aquatic and terrestrial Luciolinae fireflies (Coleoptera: Lampyridae). *Zootaxa*, *3404*, 1–34.

Gursoy, D., & McCleary, K. W. (2004). An integrated model of tourists' information search behavior. *Annals of Tourism Research*, *31*, 353–373.

Haugan, E.B. (2019). 'Homeplace of the heart': Fireflies, tourism and town-building in rural Japan. Unpublished Master's thesis, University of Oslo. https://www.duo.uio.no/handle/10852/70274

Honey, M. (2008). *Ecotourism and sustainable development: Who owns paradise?* (2nd ed.). Washington, DC: Island Press.

Hosaka, T., Kurimoto, M., & Numata, S. (2016). An overview of insect-related events in modern Japan: Their extent and characteristics. *American Entomologist*, *62*, 228–234. https://doi.org/10.1093/ae/tmw079

Hwang, Y. T., Moon, J., Lee, W. S., Kim, S. A., & Kim, J. (2020). Evaluation of firefly as a tourist attraction and resource using contingent valuation method based on a new environmental paradigm. *Journal of Quality Assurance in Hospitality &Tourism*, *21*, 320–336. https://doi.org/10.1080/1528008X.2019.1663464

IUCN (2016). *A global standard for the identification of Key Biodiversity Areas: Version 1.0. Gland, Switzerland: International Union for Conservation of Nature*. Retrieved from https://portals.iucn.org/library/node/46259

Jaikla, S., Lewis, S. M., Thancharoen, A., & Pinkaew, N. (2020). Distribution, abundance and habitat characteristics of the congregating firefly, *Pteroptyx* Olivier (Coleoptera: Lampyridae) in Thailand. *Journal of Asia-Pacific Biodiversity*, *13*, 358–366. https://doi.org/10.1016/j.japb.2020.06.002

Jeong, G.-H., Roh, Y. H., & Yhang, W. J. (2005). Visitors' perceptions to ecotourism goals and satisfaction: The case of the Muju firefly festival. *Journal of the Environmental Sciences*, *4*, 373–377.

Johansen, K., & Auger, A. (2013a). Citizen science and insect conservation. In R. H. Lemelin (Ed.), *The Management of Insects in recreation and tourism* (pp. 252–273). Cambridge, London: Cambridge University Press.

Jusoh, W. F., Ballantyne, L., Lambkin, C. L., Hashim, N. R., & Wahlberg, N. (2018). The firefly genus *Pteroptyx Olivier* revisited (Coleoptera: Lampyridae: Luciolinae). *Zootaxa*, *4456* (1), 1–7

Kawahara, A. Y. (2007). Thirty-foot telescopic nets, bug-collecting videogames, and beetle pets: Entomology in modern Japan. *American Entomologist*, *53*, 160–172.

Khoo, V., Nada, B., Kirton, L. G., & Phon, C. K. (2012). Monitoring the population of the firefly *Pteroptyx* tener along the Selangor River, Malaysia for conservation and sustainable ecotourism. *Lampyrid*, *2*, 162–173.

Laurent, E. L., & 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. https://doi.org/10.2752/089279399787000165

Lemelin, R. H. (Ed.). (2013). *The management of insects in recreation and tourism*. Cambridge: Cambridge University Press.

Lemelin, R. H., & Jaramillo-López, P. F. (2019). Orange, black, and a little bit of white is the new shade of conservation: The role of tourism in monarch butterfly conservation in Mexico. *Journal of Ecotourism*, *19*, 291–303. https://doi.org/10.1080/14724049.2019.1656726

Lemelin, R. H., Boileau, E., & Russell, C. (2019). Entomotourism: The allure of the arthropod. *Society & Animals*, *27*, 733–750.

Lemelin, R. H., Jaramillo-López, P. F., López-Ocaña, N., & Del-Val, E. (2020). In the still of the night: Firefly tourism in Mexico. *Anatolia*. https://doi.org/10.1080/13032917.2020.1819832

Lewis, S. M. (2016). *Silent sparks: The wondrous world of fireflies*. NJ: Princeton University Press.

Lewis, S.M. (2017). For the sake of their glow. *Undark Magazine* Retrieved from https://undark.org/2017/06/01/sake-their-glow-moriyama-japan-fireflies/

Lewis, S. M., & Cratsley, C. K. (2008). Flash signal evolution, mate choice, and predation in fireflies. *Annual Review of Entomology*, *53*, 293–321.

Lewis, S.M. and A.C.S. Owens (2017). China's endangered fireflies. Scientific American 2017. Retrieved from https://blogs.scientificamerican.com/observations/chinas-endangered-fireflies/

Lewis, S. M., Wong, C. H., Owens, A. C. S., Fallon, C., Jepsen, S., Thancharoen, A., ... Reed, J. M. (2020). A global perspective on firefly extinction threats. *Bioscience*, *70*, 157–167. https://doi.org/10.1093/biosci/biz157

Lloyd, J. E. (1972). Chemical communication in fireflies. *Environmental Entomology*, *1*, 265–266.

Lloyd, J.E. (2002). Family 62: Lampyridae. pp. 187–196 in: *American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea*, by R.H. Arnett, M.C. Thomas, P.E. Skelley, and J. H. Frank (eds.). CRC Press, Boca Raton, FL.

Lloyd, J. E. (2008). Fireflies (Coleoptera: Lampyridae). In J. L. Capinera (Ed.), *Encyclopedia of entomology* (pp. 1429–1452). New York: Springer.

Loomboot S. (2008). Rearing techniques and development of suitable natural environment for fireflies, *Pteroptyx malaccae* Gorham. Unpublished PhD thesis, Kasetsart University, Bangkok Thailand (in Thai).

Martin, G. J., Stanger-Hall, K. F., Branham, M. A., da Silveira, L. F. L., Lower, S. E., Hall, D. W., ... Bybee, S. M. (2019). Higher-level phylogeny and reclassification of Lampyridae (Coleoptera: Elateroidea). *Insect Systematics and Diversity*, *3*, . https://doi.org/10.1093/isd/ixz024

Napompeth, B. (2009). Reminiscence of firefly study in Thailand. In B. Napompeth (Ed.), *Diversity and conservation of fireflies: Proceedings of the international symposium on fireflies* (pp. 1–10). Chiang Mai, Thailand: Queen Sirikit Botanic Garden.

Nurancha, P., Inkapatanakul, W., & Chunkao, K. (2013). Guidelines to the management of firefly watchng tour in Thailand. *Modern Applied Science*, *7*, 8–14.

Oba, Y., Branham, M., & Fukatsu, T. (2011). The terrestrial bioluminescent animals of Japan. *Zoological Science*, *28*, 771–789. https://doi.org/10.2108/zsj.28.771

Ohba, N. (2004). *Mysteries of fireflies*. Yokosuka, Japan: Yokosuka City Museum (in Japanese).

Ohba, N., & Wong, C. H. (2012). Observations on the external morphology and behavior of *Pteroptyx tener* and *Pteroptyx bearni* in Malaysia. *Lampyrid*, *2*, 80–86.

Owens, A. C. S., & Lewis, S. M. (2018). The impact of artificial light at night on nocturnal insects: A review and synthesis. *Ecology and Evolution.*, *8*, 11337–11358. https://doi.org/10.1002/ece3.4557

Owens, A. C. S., & Lewis, S. M. (2021). Narrow-spectrum artificial light silences female fireflies (Coleoptera: Lampyridae). *Insect Conservation and Diversity* in press.

Owens, A. C. S., Meyer-Rochow, V. B., & Yang, E. C. (2018). Short- and mid-wavelength artificial light influences the flash signals of *Aquatica ficta* fireflies (Coleoptera: Lampyridae). *PLoS One*, *13*, e0191576. https://doi.org/10.1371/journal.pone.0191576

Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkins, E. K., & Seymoure, B. (2020). Light pollution is a driver of insect declines. *Biological Conservation*, *241*, 108259. https://doi.org/10.1016/j.biocon.2019.108259

Pellegrino, M., Steinbach, N., Stensmyr, M. S., Hansson, B. S., & Vosshall, L. B. (2011). A natural polymorphism alters odour and DEET sensitivity in an insect odorant receptor. *Nature*, *478*, 511–514. https://doi.org/10.1038/nature10438

Reed, J. M., Nguyen, A., Owens, A. C. S., & Lewis, S. M. (2020). Linking the seven forms of rarity to extinction threats and risk factors: An assessment of north American fireflies. *Biodiversity and Conservation*, *29*, 57–75. doi.org/10.1007/s10531-019-01869-7

Salazar, N. B. (2012). Community-based cultural tourism: Issues, threats and opportunities. *Journal of Sustainable Tourism*, *20*, 9–22.

Salerno, J., Romulo, C., Galvin, K. A., Brooks, J., Mupeta-Muyamwa, P., & Glow, L. (2021). Adaptation and evolution of institutions and governance in community-based conservation. *Conservation Science and Practice*, *3*. https://doi.org/10.1111/csp2.355

Samways, M. J. (2005). *Insect diversity conservation*. UK: Cambridge University Press.

Schreiber, R. (2017). *Firefly experience*. Grand Rapids, MI: ArtBook Printing.

Sexton, N. R., Miller, H. M., & Dietsch, A. M. (2011). Appropriate uses and considerations for online surveying in human dimensions research. *Human Dimensions of Wildlife*, *16*, 154–163. https://doi.org/10.1080/10871209.2011.572142

Shahwahid, H., Iqbal, M., Ayu, A., & Farah, M. (2013). Assessing service quality of community-based ecotourism: A case study from Kampung Kuantan Firefly Park. *Journal of Tropical Forest Science*, *25*, 22–33.

Smith, H. M. (1935). Synchronous flashing of fireflies. *Science*, *82*, 151–152. https://doi.org/10.1126/science.82.2120.151

Stronza, A. L., & Durham, W. H. (Eds.). (2008). *Ecotourism and Conservation in the Americas. Ecotourism series no. 7*. Cambridge, MA: CAB International.

Stronza, A. L., Hunt, C. A., & Fitzgerald, L. A. (2019). Ecotourism for conservation? *Annual Review of Environment and Resources*, *44*, 229–253.

Taiwan Tourism Bureau (2017). Firefly watching in Taiwan. Retrieved from https://eng.taiwan.net.tw/att/files/Firefly%20Watching%20in%20Taiwan.pdf

Thancharoen, A. (2012). Well-managed firefly tourism: A good tool for firefly conservation in Thailand. *Lampyrid*, *2*, 142–148.

Thancharoen, A., & Masoh, S. (2019). Effect of camera illumination on flashing behavior of *Pteroptyx malaccae* (Coleoptera: Lampyridae). *InTechOpen*. https://doi.org/10.5772/intechopen.85796

Thompson, B. S., & Rog, S. (2019). Beyond ecosystem services: Using charismatic megafauna as flagship species for mangrove forest conservation. *Environmental Science and Policy*, *102*, 9–17. https://doi.org/10.1016/j.envsci.2019.09.009

Thompson, B. S., Gillen, J., & Friess, D. A. (2018). Challenging the principles of ecotourism: Insights from entrepreneurs on environmental and economic sustainability in Langkawi, Malaysia. *Journal of Sustainable Tourism*, *26*, 257–276. https://doi.org/10.1080/09669582.2017.1343338

TIES (2015). *Definitions and principles*. The International Ecotourism Society, Washington, DC. Retrieved from https://ecotourism.org/news/ties-announces-ecotourism-principles-revision/

Vance, E. and S. Kuri (2017). How fireflies are keeping this tiny Mexican town alive. *National Geographic*. Retrieved from https://www.nationalgeographic.com/photography/proof/2017/08/firefly-fields-mexico-tourism-ecotourism/

Vila, T., Vila, N., González, E., & Brea, A. (2018). The role of the internet as a tool to search for tourist information. *Journal of Global Information Management*, *26*, 1–27. https://doi.org/10.4018/JGIM.2018010104

Wardle, C., Buckley, R., Shakeela, A., & Castley, J. G. (2018). Ecotourism's contributions to conservation: Analysing patterns in published studies. *Journal of Ecotourism*, 1–31. https://doi.org/10.1080/14724049.2018.1424173

Watson, A. E., & Borrie, W. T. (2003). Applying public-purpose marketing in the USA to protect relationships with public lands. In R. Buckley, C. M. Pickering, & D. B. Weaver (Eds.), *Nature-based tourism, environment, and land management. Ecotourism book series* (Vol. 1, pp. 25–33). Cambridge MA: CABI.

Wong, C. H. (2009). Firefly watching and conservation involving local communities in Malaysia. In B. Napompeth (Ed.), *Diversity and conservation of fireflies: Proceedings of the international symposium on fireflies* (pp. 141–148). Chiang Mai, Thailand: Queen Sirikit Botanic Garden.

Wong, C. H., & Yeap, C. A. (2012). Conservation of congregating firefly zones in peninsular Malaysia. *The Lamp*, *2*, 174–187.

Wood, E. H. (2019). I remember how we all felt: Perceived emotional synchrony through tourist memory. *Journal of Travel Research*, *59*, 1–14. https://doi.org/10.1177/0047287519888290

World Tourism Organization. (2019). *International Tourism Highlights, 2019 Edition*. Madrid: UNWTO. https://doi.org/10.18111/9789284421152

Xu, P., Zeng, F., Bedoukian, R. H., & Leal, W. S. (2019). DEET and other repellents are inhibitors of mosquito odorant receptors for oviposition attractants. *Insect Biochemistry and Molecular Biology*, *113*, 103224. https://doi.org/10.1016/j.ibmb.2019.103224

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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