



Like moths to a flame: A review of what we know about pyrophilic insects

Aaron J. Bell^{*}

Department of Biology, University of Saskatchewan, #112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada
 Troutreach Saskatchewan, Saskatchewan Wildlife Federation, #9 Lancaster Road, Moose Jaw, Saskatchewan S7J 1M8, Canada

ARTICLE INFO

Keywords:

Biodiversity
 Fire-dependent
 Infrared receptors
 Natural disturbance
 Pyrophilous
 Reproductive synchrony

ABSTRACT

The concurrent impacts of fire suppression, climate-warming, and industrial forestry have dramatically altered the spatio-temporal patterns of fire across the globe. Pyrophilic insects are among the species most threatened by these changes due to their dependence on recurring fire, and the extent to which they are adapted for exploiting the post-burn environment. Here, I review our current understanding of pyrophilic insects and the life-history adaptations that facilitate this highly specialized mode of life. I begin with an evaluation of three lines of evidence commonly used to characterize species' associations with fire, including pyrophilic behaviour (i.e., attraction to fire), possession of pyrophilic adaptations (e.g., infrared sensors), and abundance patterns in burnt and unburnt habitats. This evaluation shows a general incongruence between the resulting lists of pyrophilic species that may explain, in part, the varying approaches to defining pyrophily in the literature. Many insects, including non-pyrophilic species, are opportunistically drawn to fire, suggesting that attraction to fire alone is not a good indicator of pyrophily. Although the relative abundance of species considered to be pyrophilic was generally higher in burnt habitats, data limitations restricted this evaluation to a small subset of species. Evidence of pyrophilic adaptations was the best single indicator of pyrophily given that these traits reflect long-standing, co-evolution with fire. Whereas much of our limited knowledge of these species stems from studies of individual taxa, there is growing consensus that these insects are part of a larger community that have evolved to exploit reproductive advantages in the post-burn environment.

1. Introduction

Fire influences global ecosystem processes, geographic distributions of species, carbon dynamics, and the Earth's climate (Pausus and Keeley, 2009, Bowman et al., 2009). Its role in the ecological and evolutionary history of life dates to the Silurian Period (440 mya) when the invasion of plants into terrestrial environments provided the necessary fuel for combustion (Glasspool et al., 2004). Today, fire occurs wherever it is sufficiently wet enough for vegetation to grow and periodically dry enough to create conditions suitable for combustion.

Fire is destructive and poses a significant threat to life, public safety, property, and natural resources. This view prevailed in the early 20th century and prompted the development of large-scale fire management programs with the initial goal of complete fire exclusion (Arno and Allison-Bunnell, 2002, Stocks and Martell, 2016). Now, after nearly a century of extensive fire suppression, there is a growing consensus that fire is essential for sustaining many ecosystems, and that the complete exclusion of fire can have unintended consequences in these ecosystems

(Martin and Sapsis, 1992, Arno and Allison-Bunnell, 2002, Pausus and Keeley, 2009, Driscoll et al., 2010).

Ongoing efforts to manage fire have been accompanied by the rise of industrial forestry (Arno and Allison-Bunnell, 2002). Although wildfires burn an average of 2.5 million hectares annually in Canada (Government of Canada, 2022), harvesting now rivals fire as one of the major disturbances across much of the boreal forest (Pratt and Urquhart, 1994, DeLong and Tanner, 1996, McRae et al., 2001). Currently, forest management practices seek to mitigate the negative effects of conventional clear-cutting by harvesting in a manner that emulates natural disturbance patterns (Hunter, 1993, Lindenmayer et al., 2012). This is done, for example, through the retention of living trees (i.e., fire skips) and deadwood that provides legacy structures like those left by fire (Lindenmayer et al., 2012, Pinzon et al., 2013, Lee et al., 2015). Although proponents of natural-disturbance-based harvesting accept that it is not possible to completely emulate all the effects of fire (Buddle et al., 2000, McRae et al., 2001, Hyvärinen et al., 2005, Nitschke, 2005), and that some of the limitations of this approach may be ameliorated through

^{*} Address: Department of Biology, University of Saskatchewan, #112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada.
 E-mail address: aaron.bell@usask.ca.

prescribed burning (Pinzon et al., 2013, Koivula and Vanha-Majamaa, 2020), the long-term impacts of these management practices on fire-adapted species are largely unknown.

Pyrophilic species are “conspicuously favoured” by fire (*sensu* Wikars, 1997) and are among the species most threatened by management practices seeking to emulate disturbance patterns through other interventive methods. These insects colonize the fire area in large numbers, usually while it is still burning, and then disappear within a relatively short period of time (i.e., generations) following fire (Wickman, 1964, Holliday, 1984; Koivula et al., 2006, Schmitz et al., 2015). Furthermore, pyrophilic species are typically found exclusively at recent burns and are comparatively rare or absent in unburnt habitats (Kessel, 1947, Wickman, 1967, Schmitz et al., 2016). This means that, in some cases, pyrophilic species are known from only a few specimens until discovery of their strong associations with fire and the post-burn environment (Severin, 1921, Kessel, 1947, Middlekauff, 1964, Wickman, 1967).

Although the term “pyrophilic” (Greek for “fire-loving”) has been applied in a variety of ecological contexts, it is frequently used in the insect literature to refer to species that are attracted to active fire or the post-burn environment (i.e., Saint-Germain et al., 2008); however, data compiled for this review show that more than 200 insect species exhibit an attraction to fire, heat, smoke, or ash (i.e., pyrophilic behaviour, see Table 1), including numerous species with no obvious or consistent affiliation to fire (e.g., the widespread dragonfly *Plantala flavescens*). Whereas the post-burn environment provides conditions that may be suitable for non-pyrophilic species (higher temperatures, increased soil microbial activity, abundance of deadwood; see Wikars, 1997 and references therein), there is growing evidence that some species are uniquely adapted to fire and that the appropriate conditions for these species are not generated by other types of disturbance. Thus, for the purposes of this review, I refer to pyrophilic insects that depend on fire for their long-term survival as “fire-dependent” species in an effort to distinguish from “disturbance-favoured” species that are attracted to and benefit from the post-burn environment. These “disturbance-favoured” species are also attracted to other disturbances that damage or kill large numbers of host trees (e.g., windthrow, gap-dynamics, clearcuts, insect outbreaks, etc.) (Nappi et al., 2004, Wikars, 2006, Hjäältén et al., 2017).

Fire-dependent species, in the strictest sense, represent an extreme form of disturbance-adaptation that is vulnerable to management practices seeking to emulate disturbance in the absence of fire. As such, studies that do not distinguish between fire-dependent or disturbance-favoured species may draw the wrong conclusions regarding the importance of fire. For example, Saint-Germain et al. (2008) used models of age-class distribution and deadwood availability to show that the persistence of pyrophilic insects depended more on the quality of the unburnt matrix than the availability of recently burnt habitat; however,

Table 1

Number of “pyrophilic” species, listed by order according to three characteristics commonly used to measure a species’ association with fire: pyrophilic behaviour (i.e., attraction to fire, heat, smoke, or ash); pyrophilic adaptations (e.g., infrared sensors, dependence on pyrophilic fungi, reproductive synchrony, or improved olfaction for detecting smoke, etc.); and greater abundance in burnt versus unburnt habitats (standardized mean difference greater than 0).

Insect Order	Pyrophilic behaviour	Pyrophilic adaptation(s)	More Abundant in Burnt vs Unburnt
Coleoptera	181	20	25
Diptera	29	26	–
Hemiptera	13	7	2
Hymenoptera	2	1	–
Lepidoptera	1	–	–
Odonata	1	–	–
Total	227	54	27

the authors made numerous references to the “pyrophilous” beetle *Monochamus* (Cerambycidae), a genus of saproxylic species that is attracted to fire, but also occur across a wide range of other disturbance types (i.e., disturbance-favoured). Whereas *Monochamus* might be attracted to fire and benefit by increased volumes of deadwood in the unburnt matrix (Saint-Germain et al. 2008), this may not be the case for fire-dependent species that rely on recurring fires for food (Hingley, 1971, Wikars, 1997, Schmitz et al., 2010, Schmitz et al., 2016) or reproductive conditions (Evans, 1972, Chandler, 2001, Klocke et al., 2009, Schmitz et al., 2015, Tkoč et al., 2017) that are rare or absent in the unburnt matrix. Thus, while it is often difficult to gauge where species fall along the continuum of ‘pyrophily’, and the ability to do so is often limited by an incomplete knowledge of their natural history, our ability to distinguish between the obligative or facultative use of the post-burn environment by insects has direct consequences for biodiversity and conservation of fire-dependent species.

In this synthesis, I examine our current understanding of pyrophilic insects and the life-history adaptations that allow them to thrive in post-burn environments. I begin with an evaluation of species commonly associated with fire and consider the following: (1) whether species are actively attracted to ongoing fire, heat, smoke, or ash (i.e., pyrophilic behaviour); (2) whether they possess adaptive traits for the survival or exploitation of recently burnt habitats (i.e., pyrophilic adaptation); and (3) whether these species are predominantly found in post-burn habitats and in higher abundances than unburnt habitats (Wikars, 1997, Nappi et al., 2004). Species that share all three characteristics are considered fire-dependent and are the primary focus of this review.

2. Material and methods

2.1. Data collection

Many scientific articles, theses, and book chapters were examined for relevant information based on searches of the keywords (“pyrophilic*” OR “pyro*”) AND “insect*” on ISI Web of Science and Google Scholar. The reference list of selected papers, including two previous reviews that discussed various aspects of pyrophilic insect ecology (Wikars, 1997, Goodman and McCravy, 2008), were also searched for relevant articles (snowballing technique). From these studies, an extensive reference list was made with approximately 400 studies (Fig. 1) compiled from a combination of keyword searches and the snowballing technique. Collectively, these studies were used to evaluate a species’ association with fire based on three lines of evidence that are commonly used to characterize pyrophilic species: (1) pyrophilic behaviour; (2) known pyrophilic adaptations; and (3) occurrence and abundance patterns in burnt and unburnt habitats (Table 1; Fig. 1).

2.2. Pyrophilic behaviour

Studies in the reference list were examined for information or documented observations of pyrophilic behaviour. This list builds on a previous review of insects attracted to fire by Evans (1972) and includes many observations at the scene of active fires (e.g., Kessel, 1960, Wickman, 1967, Lindroth, 1969). I also scanned species lists from ecological studies examining before-after application of fire. In the pyrophilic behaviour context, a species was classified as attracted to fire if (1) it was not recorded at a site prior to fire, (2) sampling was conducted the same calendar year as the fire, (3) a minimum of five individuals were collected in the burnt treatment, (4) no individuals were collected in the unburnt treatment (see Supplemental Material 1 – Table 2). Two studies employing smoke traps in the vicinity of recently burnt forests (Sundin, 2014, Milberg et al., 2015) contributed a substantial number of species to this list (n = 142 species, 67 % of total, Supplemental Material 1 – Table 2).

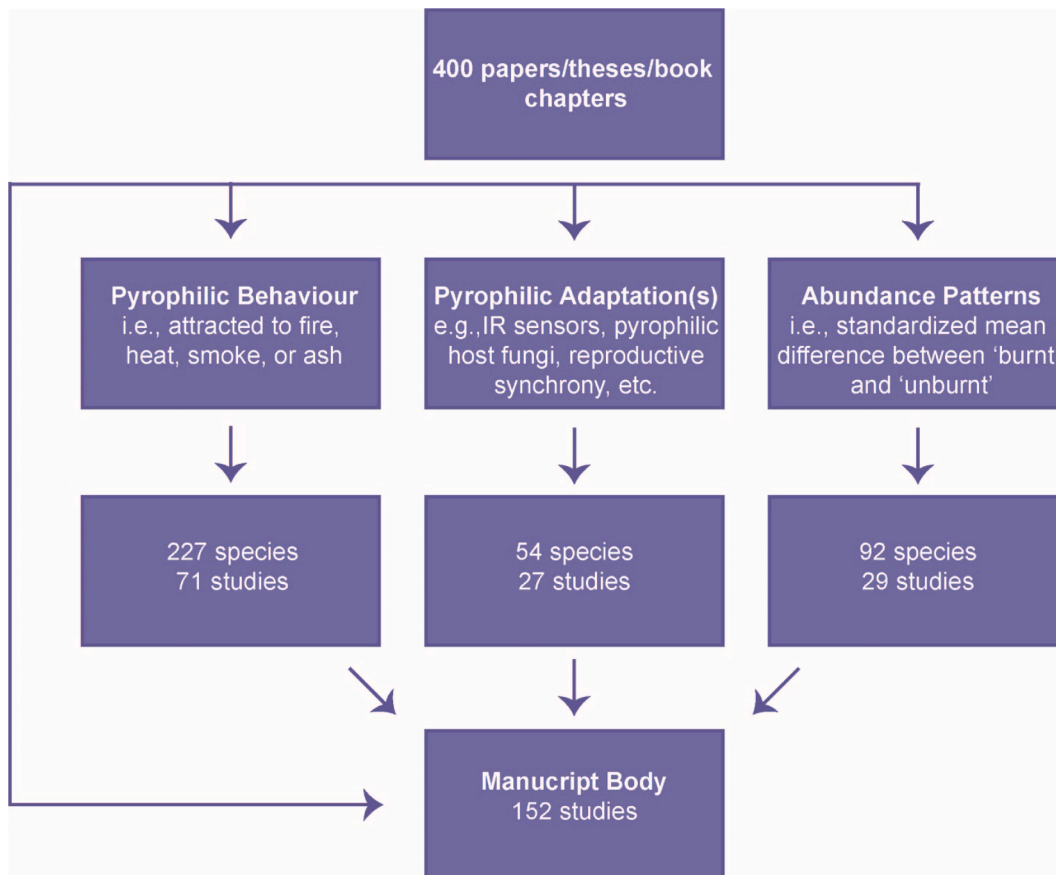


Fig. 1. Conceptual framework of the literature review.

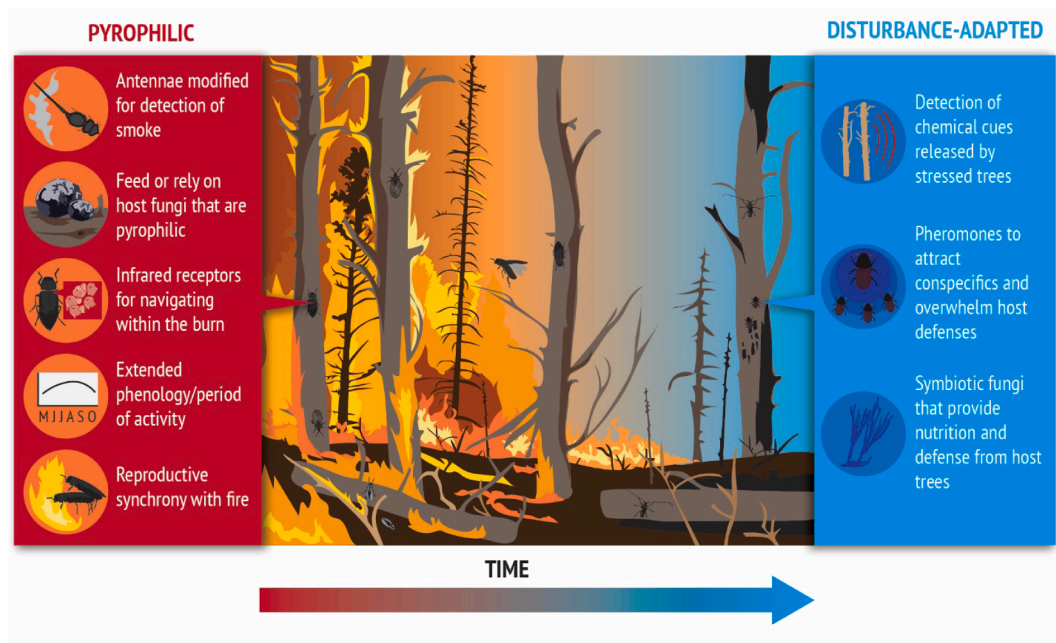


Fig. 2. Illustration depicting the colonization of an active forest fire by pyrophilic species (e.g., species from the genera *Sericoda*, *Aradus*, and *Melanophila*) and subsequent colonization by general disturbance-adapted species (e.g., *Dendroctonus*, *Monochamus*) shortly after fire. Featured adaptations for exploiting the post-burn environment (left) illustrate their strong affiliation with fire compared to more generalized adaptations shared by species associated with disturbance or stressed trees (right).

2.3. Pyrophilic adaptations

Evidence of known or suspected pyrophilic adaptations was compiled from the reference list. Broadly stated, pyrophilic adaptations include behavioural, developmental, reproductive, and/or physiological adaptations to fire and the immediate post-burn environment (Fig. 2). Examples of pyrophilic adaptations used in the current study include infrared (IR) sensors (see Schmitz et al., 2016), modified antennal morphology for the detection of smoke (Sinclair and Cumming, 2006), reproductive synchrony with fire (i.e., fire-induced reproductive behaviour, see below), dependence on host fungi that are pyrophilic (e.g., *Daldinia* spp., Hingley, 1971, Alexander, 2002), and dependence on fire-associated fungi for food and development of young (e.g., *Aradus* bugs (Aradidae), Schmitz et al., 2016).

2.4. Pyrophilic insect abundance patterns

To evaluate abundance patterns of pyrophilic species, I searched for studies containing information on the relative abundance of pyrophilic species in burnt and unburnt habitats. In this context, studies were only included if: (1) they sampled unburnt and burnt habitats using similar methodology (pitfall and flight-intercept traps); (2) the onset of sampling in the “burnt” habitat occurred within three years of the burn; and (3) information on abundance at the species-level was available in the text, appendix, or supplemental material of the article. This produced a list of 29 relevant studies (Fig. 1, Supplemental Material 2 – Tables 3 and 4). Three of the studies included two separate experiments for which data could be compared independently (Muona and Rutanen, 1994, Cobb et al., 2007, Hägglund et al., 2015), producing a total of 32 datasets. Four of these studies included multiple burn treatments (e.g., low intensity, high intensity) which were combined under a single burn treatment for analysis. Furthermore, the characteristics of the unburnt habitat varied between studies and included both unburnt, intact forest (18 studies) and unburnt forests that were subject to various levels of harvesting, thinning, or girdling (14 studies, see Supplemental Material 3 – Table 5). Because prospective pyrophilic species may respond to these two types of unburnt habitats differently, and because the level of disturbance in harvested stands is likely more like burnt habitats than unburnt unharvested controls (see Boucher, 2010), I used data from harvested treatments as opposed to unharvested controls whenever possible (see Supplemental Material 3 – Table 5).

Abundance data were collected for species classified as pyrophilic, fire-associated, fire-favoured, burn-associated, or fire-dependent in the ecological literature (see full list of studies in Supplemental Material 4). Few studies included detailed information on sampling effort at the level of individual traps (trap-days, lost traps, etc.) that would permit comparison of catch-rates among studies. Therefore, I attempted to standardize sampling effort for each study at the site-level for comparisons of abundance between burnt and unburnt habitats. This approach allowed standardized comparisons of abundances for 28 of the 32 studies, with three of the four unstandardized studies placing greater sampling effort in the unburnt habitats. Raw abundance data were used to compare abundances in burnt and unburnt habitats for the majority of studies ($n = 27$), whereas mean or median abundances were used in the remaining five studies to allow standardized comparisons. Detailed information on how abundance data were collected from each study is available in the Supplemental Material 3 – Table 5.

Abundance patterns in burnt and unburnt habitats were compared using standardized mean difference (Cohen’s d), calculated as the difference between means (burnt and unburnt) divided by the pooled standard deviation. Given the general paucity of data for most species, standardized mean difference was only reported for species with at least four independent data points (i.e., studies). Confidence intervals ($\alpha = 0.2$) were calculated using non-parametric bootstrapping with replacement, in which abundances for each species were sampled 1000 times from the original data. Analysis of species’ abundance patterns

were conducted in R (R Core Team 2021) using the Cohen’s d function in Kelley (2005) and dplyr (Hadley et al., 2021), tidytext (Silge and Robinson, 2016), and forestplot (Gordon and Lumley, 2021) packages in R. The full reproducible code is available in the Supplemental Material 5.

3. A brief analytical perspective on “Pyrophily”

Distinguishing between the obligative or facultative use of the post-burn environment is challenging, partly because the criteria for assessing a species’ association with fire varies between studies (Lundberg, 1984, Wikars, 1997, Saint-Germain et al., 2008). A review of three common approaches to this question demonstrates a general incongruence between the resulting lists of pyrophilic species (Table 1). For example, evidence for an attraction to fire was documented in more than 200 species, including many non-pyrophilic species (Supplemental Material 1 – Table 2). These non-pyrophilic species are likely capable of detecting smoke-volatiles, albeit at much higher concentrations than pyrophilic species (see section 5.1 Olfaction), and are opportunistically attracted to fire. Therefore, the assumption that only pyrophilic species are attracted to fire, and that such attraction is indicative of a species’ affinity for fire is questionable. As such, attraction to fire alone is a poor indicator of pyrophily.

Abundance data were gathered for 92 prospective pyrophilic species; however, limitations in available data meant that meaningful comparisons between burnt and unburnt habitats were only possible for 29 species. Of these species, only two had SMD values that were indicative of higher abundances in unburnt habitats (Table 1; see Supplemental Material 1 – Table 2.). The remaining 27 species had SMD values that indicated higher abundances in burnt habitats (Table 1, Fig. 3); however, these results should be treated with caution due to data constraints and variation in the experimental design of studies from which the data was gathered (see section 2.4 Materials and Methods). Only two species, *Sericoda quadripunctata* (Carabidae) and *Pterostichus adstrictus* (Carabidae), had greater than seven studies from which to draw abundance data (Fig. 3). Additional evidence of pyrophily was documented for *Sericoda quadripunctata* (i.e., attraction to fire and pyrophilic adaptations) but not for *Pterostichus adstrictus*. The latter species is considered pyrophilic by some authors (Hjältén et al., 2010, Hekkala et al., 2015) but is also one of the most abundant beetles in unburnt, mature coniferous forests in Canada (Lindroth, 1969, Bell et al., 2017). Because abundance data were only included if burnt and unburnt habitats were sampled in the same study, studies that focused exclusively on unburnt habitats were not included. These methodological constraints and general limitations of abundance data available in the literature suggest that this approach to assessing associations with fire should only be used in concert with other evidence of pyrophily (e.g., attraction and adaptations, Fig. 3).

Documented evidence of a pyrophilic adaptation is probably the best single indicator of pyrophily. These adaptations result from co-evolution with fire (e.g., infrared sensors) and reflect a long-term dependence on food, reproductive conditions, or host fungi that are rare or absent from the unburnt matrix (Fig. 3; Supplemental Material 1 – Table 2). Extensive study of some groups (Coleoptera, Diptera, and Hemiptera, Table 1) have even documented multiple pyrophilic adaptations within individual species (Fig. 3), reflecting a highly specialized strategy for thriving in post-burn environments that is consistent with long-term dependence on fire. Based on this approach, a total of 55 species are considered pyrophilic, although additional, undocumented pyrophilic adaptations undoubtedly exist. Interestingly, classification of these 55 species as pyrophilic is also supported by evidence of an attraction to fire and greater abundances in burnt habitats. Collectively, this evaluation suggests that all three approaches should be considered when evaluating whether a species is pyrophilic, but attraction to fire and higher abundances in burnt habitats are poor indicators of fire-dependence. However, evidence of attraction to fire or greater abundance in burnt habitats might also be used to guide future investigations into pyrophilic adaptations (e.g., infrared sensors) among prospective pyrophilic

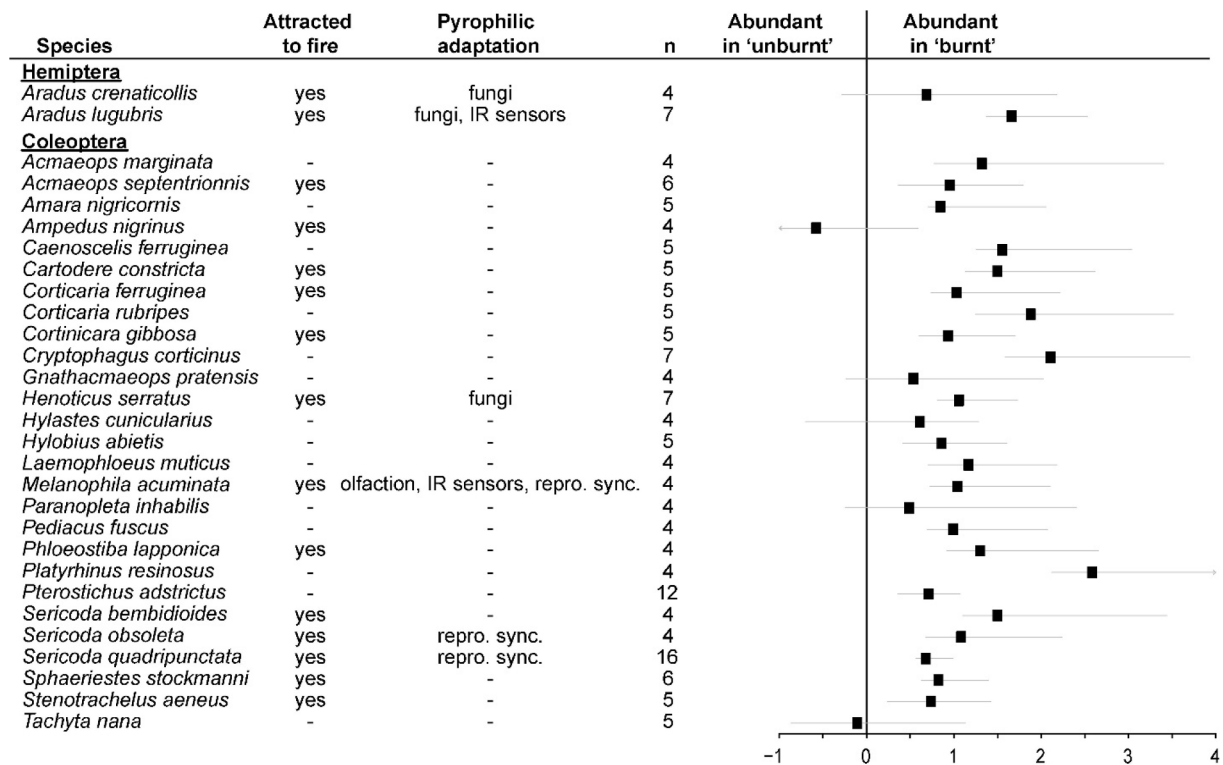


Fig. 3. A three-pronged approach for evaluating a species' affinity for fire and the post-burn environment based on whether they are actively attracted to fire, possess known pyrophilic adaptations (see Table 1), and occur in higher abundances in burnt habitats (standardized mean difference [SMD] \pm 80 % confidence interval) based on a review of the ecological literature. SMD values greater than zero indicate abundances are higher in burnt habitats, whereas values less than zero indicate the opposite. Species with fewer than four studies containing abundance information (n) were omitted. Note that lower and upper confidence intervals for *Ampedus nigrinus* (-1.28) and *Platyrhinus resinus* (6.15) were truncated for display purposes.

species.

4. Attraction to fire and behaviour in the post-burn environment

4.1. Rapid colonization and local abundance

The peculiar and remarkable attraction of pyrophilic insects to fire and their behaviour in the post-burn environment is perhaps best illustrated in the many written accounts and detailed descriptions of first-hand observations. Collectively, these observations demonstrate that fire-dependent species colonize the active fire area quickly, usually in large numbers while the fire is still burning, and then disappear within a relatively short period of time (i.e., generations). In one of the earliest records of this phenomenon, Ricksecker (1885) found hundreds of *Melanophila acuminata* (Buprestidae) and *Melanophila consputa* swarming a small patch of Douglas fir that had been scorched by a brush fire. Similarly, Wickman (1964) documented the arrival of *Melanophila consputa* at an active fire, noting that peak abundance occurred in the first two days of the fire and declined sharply by the fourth day when the fire was extinguished. Tepper (1887) noted that under normal conditions, the pyrophilic beetle *Merimna atrata* (Buprestidae) is difficult to find and, unlike many other buprestids, could never be found at flowers. He noted areas that were previously free of *Merimna atrata* could be swarming with thousands of beetles only hours after a brushfire (Tepper, 1887). Visiting a freshly burnt area with assistance from local fire-fighters in Australia, Schmitz et al. (2015) documented the arrival of *Merimna atrata* in large numbers while the fire was still active, noting that peak abundance occurred on the first day of the fire and gradually declined until the fourth day when no beetles could be found.

Pyrophilic ground-beetles from the genus *Sericoda* also appear, often suddenly, in great numbers during forest fires and then disappear one to three years following the fire (Lindroth, 1969, Burakowski, 1986,

Holliday, 1984, 1991, Koivula et al., 2006, Fredriksson et al., 2020). Following a long day assisting fire-fighters on the frontlines of a large fire in central Canada, I. Phillips observed large numbers of *Sericoda obsoleta* descending from the smoke-filled sky and landing in a parking lot several kilometres from the fire's edge. Hundreds of *Sericoda obsoleta* clustered near firefighting equipment and crawled into smoke and sweat-laden overhauls (I. Phillips personal communication), possibly attracted to the smoke-saturated clothing as observed in smoke flies (Platypozidae: *Microsania*, see Kessel, 1960). Visiting a burnt forest, still smoldering after recent fire, Bell et al. (2022) found hundreds of very active *Sericoda obsoleta* running along the ground, which was covered in a thick (10–12 cm) layer of ash. Revisiting the area at roughly weekly intervals, Bell et al. (2022) showed that the abundance of *Sericoda obsoleta* declined in the burnt area after 18 days, and that this decline coincided with the arrival and peak abundance of a second pyrophilic species, *Sericoda quadripunctata*. Whether the staggered arrival of *Sericoda obsoleta* and *Sericoda quadripunctata* in the post-burn environment relates to the distance of source populations (i.e., other recent burns) or a temporal partitioning of habitat is unknown (but see section Dispersal 5.3).

Observations at active fires have also been important for establishing the link between seemingly rare pyrophilic species and their association with fire. Prior to the discovery of their attraction to smoke, "smoke flies" from the genus *Microsania*, were considered very rare, and until 1934, only six specimens were known from England (Kessel, 1947). In an area where he had collected insects diligently for twenty years without capturing a single specimen, Severin (1921) found many *Microsania stigmatalis* swarming above a smoldering heath fire, noting that the flies did not stray far from the burning area. Kessel (1947) also failed to collect *Microsania* outside of burnt areas, despite significant efforts to do so. Upon returning from a disappointing collecting trip to Humboldt County in California where the State's only record of the

genus had been reported, he collected more than a dozen *Microsania occidentalis* that were attracted to the smoke of his backyard barbecue (Kessel, 1947). The tendency to find seemingly “rare” species in much greater numbers at active fires is also true for the cedar wood wasp, *Syntexis libocedrii* (Anaxyelidae). Prior to the collections by Wickman (1964, 1967) at a forest fire in northern California, the cedar wood wasp, *Syntexis libocedrii* was only known from a series of three female specimens (Middlekauff, 1964). After discovering its association with fire, more than 90 individuals of *Syntexis libocedrii* were collected from recently burnt sites over a four-year period, including the previously undescribed male (Middlekauff, 1964, Wickman, 1967).

It is important to note that numerous pyrophilic species have also been observed in areas with no obvious fires or smoke in the immediate vicinity. For example, Russell (1960) observed aerial swarms of the male smoke fly, *Microsania pectipennis*, near the upper branches of a tree in England with no signs of smoke nearby. Evans (1972) found larvae of *Melanophila acuminata* in unburnt spruce that had been cut during the summer in Canada. The fire-associated fungus *Daldinia* (Xylariaceae) is an important host for some pyrophilic insects like *Henoticus serratus* (Cryptophagidae) (Wikars, 1997), but the fungus is also found, albeit less commonly, on unburnt trees (Hingley, 1971, Johannesson et al., 2000) and thus may provide habitat for pyrophilic species outside of fires. Reports of pyrophilic species in camping tents (Melander, 1922), ceiling lights (Kessel, 1947, 1952), and in and around human dwellings (Lindroth, 1992) are also common, although these occurrences might be explained by their proximity to campfires, wood-burning stoves (Chandler, 2001, Larochelle and Larivière, 2003), or forest fires. Thus, while pyrophilic species can occasionally be found outside of burnt areas, sightings are usually rare and only a few individuals are reported.

4.2. Tolerance to extreme heat and attraction to anthropogenic sources

Numerous first-hand accounts also note an apparent high tolerance to heat and the ability of fire-dependent insects to navigate the thermally complex environments typical of an active fire. Sharp (1918) described collecting *Melanophila acuminata* from a burning pine stump, noting that many of the beetles were running on ground that was too hot to touch. Using a tungsten wire heated 5 °C above ambient temperature, Evans (1972) showed that captive adults of *Melanophila acuminata* were attracted to the wire and remained near it for long periods. Lindroth (1969, 1972) describes seeing beetles of the genus *Sericoda* flying towards a raging forest fire, landing directly on burning wood, or settling among hot ashes. Well-camouflaged on the black background of burnt bark, Schmitz et al. (2015) reported that newly arriving *Merminia atrata* were seen basking in full sunlight on the sun-exposed, burnt sections of eucalyptus trees, notably avoiding shaded stems and branches.

Responding to inquiries and complaints from operators, Linsley (1943) and others discovered that numerous *Melanophila* species were attracted to the heat and smoke given off by oil fires (Van Dyke, 1926), cement and smelter plants (Champion, 1918, Linsley 1933, 1943, Linsley and Hurd, 1957, Scholtz and MacRae 2016), wood-scrap burners (Evans, 1962), and sugar refineries (Van Dyke, 1928). At two cement plants in California, Linsley and Hurd (1957) noted large numbers of *Melanophila consputa* and *Melanophila occidentalis* congregated near “hot spots” around the plant where air temperature regularly exceeded 50 °C. Incidentally, the observations made at these man-made structures helped establish that heat and smoke (and associated volatiles) were important components in the attraction of insects to fire (Linsley, 1943). These structures also served as reliable locations for the collection and study of pyrophilic species that might otherwise be challenging to find given the irregular occurrence of forest fires.

4.3. Reproductive behaviour associated with the post-burn area

Many observations made at active fires or in the immediate aftermath also document peculiar reproductive behaviour among pyrophilic

insects in the post-burn environment. For instance, Schmitz et al. (2015, 2016) observed females of two pyrophilic species, *Merminia atrata* and *Acanthocnemus nigricans* (Acanthocnemidae), “diving” into ash with the tip of their abdomen only a few meters away from the base of burnt trees, likely depositing eggs there or near roots that were damaged by fire (Schmitz and Schmitz, 2020). They also noted that after more than a decade of studying *Merminia atrata* in post-burn areas, they have never seen females deposit eggs in the unburnt portion of a tree (Schmitz et al., 2015). Similar preferences for oviposition in burnt trees has also been reported for *Melanophila* beetles (Wickman, 1964, Schmitz and Bleckmann, 1998, but see Evans, 1972), the beetle *Stephanopachys linearis* (Bostrichidae) (Ranius et al., 2014, Borowski et al., 2018), and the cedar wood wasp, *Syntexis libocedrii* (Wickman, 1967). In *Syntexis linearis*, the larvae only develop in the region between the living and dead cambium of scorched living trees where fire-scar tissue is actively formed (Ranius et al., 2014). Similarly, experimental rearing of captive *Syntexis libocedrii* wasps in cages demonstrated that females only oviposit and produce larvae from burnt logs, as no oviposition was observed on unburnt logs (Wickman, 1967). In contrast to these studies showing a preference for ovipositing in burnt trees, Cadorette-Breton (2014) found that females of the disturbance-adapted species, *Monochamus scutellatis*, showed no preference for ovipositing in either burnt or unburnt black spruce logs (*Picea mariana*, Pinaceae).

Upon arrival at the source of smoke, male *Microsania* flies assemble in swarms above the drifting smoke plume (Edwards, 1934, Snoddy and Tippins, 1968, Chandler, 2001). While observing a sawmill whose incinerator and burning waste material attracted the flies, Snoddy and Tippins (1968) described swarms of *Microsania imperfecta* as spherical, about one to two feet in diameter, and containing hundreds of male flies. Recorded temperatures within the smoke plume (40–65 °C) were well-above ambient temperature (18 °C) and changes in orientation of the smoke plume caused the swarm of flies to shift accordingly to remain within the smoke (Snoddy and Tippins, 1968, Klocke et al., 2011). Females entering the swarm were quickly grasped by males mid-flight and mating pairs settled onto the ground below, remaining in copulo for up to a minute (Snoddy and Tippins, 1968). Although several studies have observed females or mating pairs of *Microsania* settling among the hot ashes (Morley, 1938, Collart, 1958, Chandler, 1978, Klocke et al., 2011), the larval habitat of all *Microsania* species are completely unknown and it is unclear whether they oviposit on burnt material (Chandler, 2001, Sinclair and Cumming, 2006). Association with the remnant ashes of fire have also been documented in other fire associated Diptera, including *Anabarynchus hyalipennis* (Therevidae), *Hypocericus nearcticus* (Phoridae), and *Astiosoma rufifrons* (Asteiidae) (Chandler, 1992, Chandler, 2001, Klocke et al., 2011), although clear signs of oviposition among the ashes have only been observed in *Anabarynchus hyalipennis* (Klocke et al., 2009, 2011).

5. Adaptations for locating and navigating to fires

5.1. Olfaction

The ability of pyrophilic insects to quickly locate fires and to disperse between burnt habitats over large geographical distances suggests that they possess exceptional sensory adaptations for locating and approaching ongoing fires. Although most insect antennae are probably equipped with thermo- and chemoreceptors capable of detecting the heat or smoke emitted from a forest fire (Table 1, Altner and Loftus, 1985), Schütz et al. (1999) demonstrated that the antennae of pyrophilic *Melanophila acuminata* were more than ten times as sensitive to guaiacol (a phenolic compound in wood smoke) than the antennae of *Phaenops cyanea* (Buprestidae), a forest pest that occasionally breeds in fire-damaged trees. When compared to two other species with no attraction to fire-damaged trees (*Ips typographus* (Curculionidae) and *Lep tinotarsa decemlineata* (Chrysomelidae)), the antennae of *Melanophila acuminata* were over 100 times more sensitive to guaiacol (Schütz et al.,

1999). These findings suggest that *Melanophila acuminata* uses olfaction to detect smoke volatiles emitted from fire-damaged trees and that it can do so at much lower concentrations than species who are not dependent on fire (Schütz et al., 1999).

Additional studies of the olfactory senses of pyrophilic insects suggest that the composition of smoke volatiles emitted from a fire provide important olfactory cues about prospective host plants and the extent of combustion of individual trees. *Merimna atrata*, for example, is highly sensitive to the main components of eucalyptus oil (Eßinger et al., 2010, Paczkowski et al., 2011) and is attracted to fires that burn eucalyptus trees; however, it is not typically attracted to fires in pure *Banksia* (Proteaceae) forests or plantations (Schmitz et al., 2015). Experimental evidence from olfactory studies in a different pyrophilic species, *Melanophila consputa*, suggests that beetles can discern the quality or condition of wood beneath the bark through certain volatiles that are released at various stages of thermal oxidation (Paczkowski et al., 2013). Such olfactory capabilities would theoretically allow beetles searching for an oviposition site to distinguish between intact, heated, and burnt wood beneath the bark of individual trees (Paczkowski et al., 2013).

Morphological investigations of the antennae have shown that some pyrophilic species possess additional sensory structures that may assist in locating fire (Schmitz and Schmitz, 2021). For example, smoke flies from the genera *Hormoepa* (Empididae) and *Microsania* each possess a pair of sensory pits, thought to be used in the detection of smoke, on the postpedicel of the antennae (Sinclair and Cumming, 2006). Furthermore, examinations of the mouthparts and antennae of the pyrophilic fly, *Hypocerides nearcticus* (Phoridae), revealed numerous olfactory chemoreceptors whose ultrastructural properties were consistent with CO₂ receptors found in other insects (Klocke et al., 2009). Because forest fires release large amounts of CO₂, it may serve as a marker for insects approaching ongoing fires or freshly burnt habitats (Klocke et al., 2009). Recent investigations of the antennae of *Merimna atrata* have revealed a secondary group of sensilla that assist in the detection of smoke (Schmitz and Schmitz 2021). These sensilla are concealed within a protective cavity that likely opens during flight, thereby preventing contamination and desiccation of the sensilla (Schmitz and Schmitz 2021). Additional

study of the olfactory capabilities of pyrophilic insects is warranted.

5.2. Infrared sensors

The existence of infrared (IR) receptors in some groups of pyrophilous insects is perhaps the most striking example of an adaptive response to exploiting recently burnt habitats. These extra-antennal IR sensors are known in 19 species and given their observed structural and functional differences, are thought to have evolved independently in all four genera (8.2 in Schmitz et al., 2016, Hoang, 2020, Supplemental Material 1 – Table 2).

In *Melanophila* beetles, the IR sensors are confined to a pair of metathoracic pits that consist of bundles of small dome-shaped sensilla (Fig. 4a, Evans, 1964, Schmitz and Bleckmann, 1997, Schmitz et al., 1997). Each sensillum consists of a cuticular sphere that is innervated by a small, ciliary dendrite. Infrared light is absorbed by the dome-shaped sensilla causing the underlying cavity to warm and expand, which, in turn, increases the inner pressure of the chamber and lateral compression of the dendrite (Schmitz et al., 2016). The IR sensors found in *Aradus* flat-bugs are functionally similar to *Melanophila*, although the sensilla are more loosely distributed on the prothorax and mesothorax and vary slightly in morphology of the cuticular sphere (Fig. 4b, Schmitz et al. 2010, 2016, Klocke and Schmitz, 2012). Because the heating of the sphere effectively converts IR radiation into a mechanical stimulus, the IR sensors in *Melanophila* and *Aradus* are considered photomechanic IR sensors and are thought to have evolved from ordinary cuticular mechanoreceptors (Vondran et al., 1995, Schmitz and Bleckmann, 1998, Klocke and Schmitz, 2012, Schmitz et al., 2016).

In *Acanthocnemus nigricans*, the IR sensors are located on a pair of prothoracic discs that are suspended above an air-filled cavity by a small stalk originating at the border of the procoxae (Schmitz et al., 2002, Kreiss et al., 2005). The outer surface of each disc is equipped with roughly 90 small (Fig. 4c), cuticular sensilla with each sensillum consisting of a poreless outer peg that is innervated by an electron-dense rod whose function remains unknown (Kreiss et al., 2005, Schmitz et al., 2016). Current understandings of this organ suggest that the sensilla

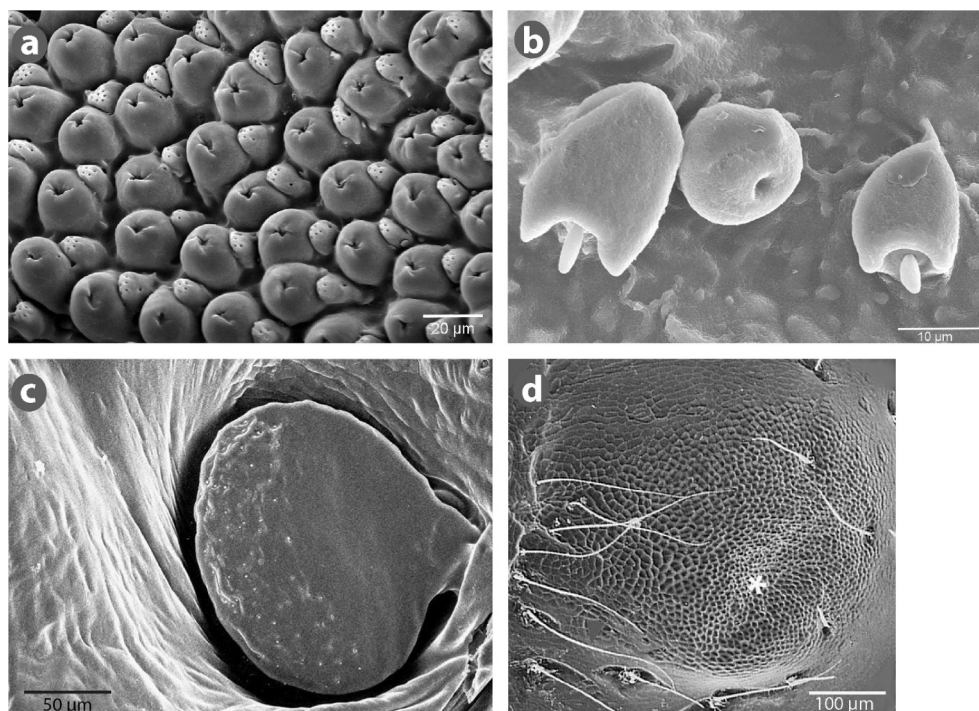


Fig. 4. Scanning electron micrograph of the four different types of infrared sensors currently known: (a) *Melanophila* spp., (b) *Aradus albicornis*, (c) *Acanthocnemus nigricans*, and (d) *Merimna atrata*. The asterisk in (d) marks the location where the multipolar neuron is attached to the inner surface of the cuticle.

have a thermosensory function and measure changes in temperature that result from absorption of IR radiation (Kreiss et al., 2005). Because each disc is suspended above an air-filled cavity, and thereby thermally insulated from the beetle's body, the sensory disc can warm or cool rapidly depending on the stimulus (Kreiss et al., 2005, Schmitz et al., 2016).

The IR sensors of *Merimna atrata* (Fig. 4d) are functionally similar to those found in *Acanthocnemus nigricans*, although they are located instead on the second, third, and occasionally the fourth abdominal sternite of the beetle (Mainz et al., 2004). Here, the radiation-absorption area consists of a roundish, shallow dint in the cuticle that is thin, lacks dark cuticular pigment, and is arranged in a honeycomb-like micro-sculpture that overlays the underlying sensory complex (Schmitz et al., 2000, 2001, Schneider and Schmitz, 2013, 2014). The lack of cuticular pigment (i.e., melanin) around the sensor is thought to reduce the absorption of visible light and enhance absorption of IR (Schmitz et al., 2001). The sensory complex of the cuticular structure consists of a large, multipolar neuron and its mass of dendrites located near a mechanosensitive chordotonal organ comprised of two scolopidia (Schneider and Schmitz, 2013; Schmitz et al., 2016). Electrophysiological investigations of the multipolar neuron indicate a thermosensory function similar to the IR sensors found in *Acanthocnemus nigricans* (Schmitz and Trenner, 2003); however, structural features at the innervation site suggest that the sensitivity of the neuron is further enhanced by minute thermal deformations that are measured by the chordotonal organ (Schneider and Schmitz, 2013). As such, the IR sensors of *Merimna atrata* likely possess both thermosensory (multipolar neuron) and photomechanical (chordotonal organ) properties that function in concert to increase the performance of the IR organ (Schneider and Schmitz, 2013, Schmitz et al., 2016).

The evolution of IR sensors among distantly related groups of pyrophilic insects and the range of structural and functional differences in these organs raises the question: what is the primary function of these sensory organs? Initially, Evans (1964, 1966) suggested that the IR sensing capabilities of *Melanophila acuminata* would allow detection and orientation towards distant fires. Since then, the “long-range orientation hypothesis” has been repeated extensively across the literature and considered the primary function of IR sensors (Schmitz et al., 1997, Goodman and McCravy, 2008, see Evans, 2010 and references therein, Schmitz and Bousack, 2012). However, current estimates of the minimum threshold sensitivity of the IR sensors in *Melanophila* (60–100 $\mu\text{W}/\text{cm}^2$ behavioural, Evans, 1966; 5 mW/cm^2 electrophysiological Schmitz and Bleckmann, 1998) are insufficient for detecting an IR signal whose intensity declines sharply with increasing distance from its source (i.e., a distant fire, Evans, 2010). This suggests that an IR signal emitted from a distant forest fire would be too weak for the IR sensors in *Melanophila* to detect (Evans, 2010). Although the IR sensors may be more sensitive than current estimates suggest (Schneider et al., 2015, see Hinz et al., 2018), it is possible that *Melanophila* relies mainly on its olfactory senses for locating distant fires, as it is readily attracted to smoke traps (Sundin 2014, listed as *Oxypteris acuminata* in Milberg et al., 2015) and possesses exceptional olfactory capabilities (see above, Schütz et al., 1999).

An alternative explanation to the long-range orientation hypothesis is that the IR sensors are used primarily for short-range detection of hotspots at an active fire (Schmitz and Trenner, 2003). According to this explanation, IR sensors assist pyrophilic insects in navigating the hazardous conditions associated with a patchy thermal environment (Schmitz and Trenner, 2003, Kreiss et al., 2007, Evans, 2010, Schmitz et al., 2016, Hinz et al., 2018). The “short-range avoidance hypothesis” is supported by several lines of evidence. First, electrophysiological recordings have shown that the IR sensors in *Aradus* bugs (11 mW/cm^2 , Schmitz et al., 2008), *Acanthocnemus nigricans* (11–25 mW/cm^2 , Kreiss et al., 2007), and *Merimna atrata* (40 mW/cm^2 , Schmitz and Trenner, 2003) are even less sensitive than in *Melanophila* and can handle much higher intensities and prolonged exposure before the sensilla become

saturated (Schmitz and Trenner, 2003, Kreiss et al., 2007, Schmitz et al., 2008). These functional properties are consistent with close-range detection of hot spots at a fire. Second, many reports have noted the apparent tendency for pyrophilic insects to approach active fires and to engage in flying, swarming, and mating behaviour near open flames (see above). This behaviour is consistent with the adaptive benefits that short-range extra-antennal IR sensors might provide and illustrates a potential selective pressure for the evolution of IR sensors (i.e., rapid arrival to and navigation of the hazardous burn areas, Schmitz et al., 2016). Third, recent behavioural studies in *Merimna atrata* have demonstrated clear avoidance behaviour when exposed to an IR stimulus, including “weak” signals that might be emitted from distant fires (Hinz et al., 2018).

The apparent attraction of a wide range of species to smoke and other fire-associated volatile cues (227 species, Table 1) also cast doubt on the long-range orientation hypothesis. The findings reported in this review (Table 1) suggest that many insect groups possess olfactory systems capable of detecting cues associated with fire. If the primary function of IR sensors is to detect and assist in navigation towards distant fires, as the long-range orientation hypothesis suggests, why would selection favor development of a completely new sensory array (i.e., IR sensors) if some pre-existing capability of detecting distant fires is already present among most insect groups? Furthermore, investigations of the olfactory systems of pyrophilic species (e.g., guaiacol in *Melanophila*, see above) clearly show improved capabilities over non-pyrophilic species, suggesting that selection has favoured the ability to detect very low concentrations of fire-associated volatiles via olfaction (Schütz et al., 1999), even in a species that has evolved highly specialized IR sensors.

5.3. Dispersal

The unpredictability of fire and the fact that recently burnt habitats are only viable for a short period of time suggests that pyrophilic insects must disperse quickly over considerable distances to find new habitats (Ranius et al., 2014). Extrapolating from studies on the source-sink dynamics of the fire-dependent black-backed woodpecker (*Picoides arcticus* (Picidae), Hutto, 1995), Nappi et al. (2004) suggested that populations of fire-dependent species might be maintained by recently burnt areas. Under this view, unburnt habitats support ‘sink’ populations that result from emigration when the burnt habitat becomes unsuitable (Nappi et al. 2004). This hypothesis has not been formally tested, although a recent study found more than twice the number of pyrophilic species in landscapes with shorter rather than longer histories of intensive forest management (Kouki et al., 2012), suggesting that the ability of pyrophilic species to colonize recently burnt habitats depends on the proximity of source populations.

To determine how far successive generations of pyrophilic insects need to travel between fires, Saint-Germain et al. (2008) measured the distance between 144 fire events (manmade fires excluded) occurring over 27 years in a forest with an estimated fire cycle of 191 years. They showed that the average distance between fires occurring one and two years apart was 38.5 km and 27.4 km, respectively, and suggested that this was too far for pyrophilic insects to travel (Saint-Germain et al., 2008). In contrast, Schmitz and Bousack (2012) showed that the “untold numbers” of *Melanophila consputa* that were attracted to a 750,000-barrel oil-tank fire in Coalinga, California (see Van Dyke, 1926) likely originated from the nearest coniferous forests 80 km to 130 km away. Indirect measures of dispersal capability were also provided by Linsley and Hurd (1957) based on observations of *Melanophila* at cement plants whose nearest coniferous forests were approximately 32 km and 64 km away. Although these latter studies provide only an indirect measure of dispersal, the provenance of *Melanophila* being the nearest coniferous forests is reasonable given the extreme aridity and lack of suitable host species in the intervening matrix (Linsley and Hurd 1957, Schmitz and Bousack, 2012).

Studies of dispersal in non-pyrophilic saproxylic insects (e.g., bark

beetles) suggest that they are capable of flying distances of 30 km or more, especially under favorable wind conditions (Atkins, 1961, Jactel and Gaillard, 1991, Bryers, 2000, Jackson et al., 2008, Chase et al., 2017). Although direct estimates of dispersal capability in pyrophilic insects are not available, physiological studies comparing flight aerodynamics suggest that they are even better dispersers than their non-pyrophilic counterparts. For example, Paarmann (1966) found that the pyrophilic species *Pterostichus quadriveolatus* (= *P. angustatus*, Carabidae) had a larger wing size despite its smaller body size when compared to the non-pyrophilic species *Pterostichus oblongopunctatus* (Carabidae). Similarly, in his comparison of three buprestid species whose breeding habitat spans a gradient of longevity, Wikars (1997) found that *Melanophila acuminata* had more flight muscles and a lower wing load (i.e., body mass-to-wing-area ratio) than the two non-pyrophilic buprestids, *Phaenops cyanea* and *Phaenops formaneki* (Buprestidae). Furthermore, wing load was negatively correlated with habitat persistence, suggesting a relationship between dispersal capability and overall residence time of breeding habitats (Wikars, 1997). A lower wing load is generally more favorable for long-distance dispersal as it requires less power to generate lift and makes flight more stable and energy efficient (Norberg, 1990, 1995, Davis and Holden, 2015).

As numerous studies have pointed out, navigation towards a distant fire could necessitate flying upwind, thereby presenting significant challenges to long-range dispersal (Saint-Germain et al. 2008, Schmitz and Bousack, 2012). This is because the directionality of a drifting smoke plume is governed by prevailing winds (Ghoneim et al., 1993) that carry smoke and associated volatile cues downwind of the fire. Assuming detection of these cues is the primary means of locating distant fires (see above), pyrophilic insects would potentially have to fly against the wind to reach the fire. However, given the paucity of information on dispersal capabilities, the relative simplicity of this argument (e.g., wind direction may change throughout the duration of a single fire), and the low concentrations of smoke volatiles that are detectable by pyrophilic insects (e.g., a few parts per billion, Schütz et al., 1999), it is unclear if only individuals caught in the drifting smoke plume are able to detect smoke from distant fires. Experimental studies making use of smoke traps near recent burns (e.g., Sundin, 2014, Milberg et al., 2015), for example, could provide valuable insights regarding these questions and the overall dispersal capabilities and spatial dynamics of pyrophilic insect populations.

6. Evolution of pyrophily in insects

The post-burn environment provides a range of advantages to newly colonizing insects (availability of deadwood, increased ambient temperatures, etc.) that likely explain the opportunistic attraction and use of this habitat by disturbance-adapted and non-pyrophilic species alike (Figs. 2 and 3). What then explains the tendency for some pyrophilic species (i.e., fire-dependent) to occur and breed exclusively in recently burnt forests? Until recently, most proposed explanations have only considered this question for individual taxa rather than in the context of the entire pyrophilic insect community. For example, to explain the sudden appearance of *Sericoda* spp. at active fires, carabidologists suggested that these species live in rodent nests and are driven to the surface by fire (Lindroth, 1992). Early studies in *Melanophila* proposed that trees scorched by fire might prevent the volatile protective substances of the tree from killing invading larvae (Poulton, 1915). Whereas the latter theory may apply to pyrophilic species that oviposit in wood, it does not explain the adaptive significance of pyrophily in species that oviposit in soil (e.g., *Sericoda* spp., Burakowski, 1986).

Wikars (1997) suggested that pyrophily evolved because the rapid colonization of the burnt environment facilitates competitive release from intraguild predation. In a survey of both burnt, clear cuts and burnt, uncut forests, he found *Sericoda quadripunctata* among most of the burnt uncut sites but not in any of the 17 surveyed clear cuts that were burnt after cutting. He argued that because the fire was not hot enough

to kill open-habitat specialists that colonized the area after logging, *Sericoda quadripunctata* was unable to successfully establish (Wikars, 1995). An alternative explanation not considered by Wikars (1995), is that the removal of fuel prior to burning may have produced a weaker “signal” (i.e., smoke) that may not have been sufficient to attract large numbers of *Sericoda quadripunctata*.

Evans (2010) and Schmitz et al. (2016) suggested that IR sensors serve a reproductive role as they help navigate the thermally complex burn environment of the active fire. Making observations at an active fire in Australia, Schmitz et al. (2015) noted that the heat and smoke of the active fire protected *Merimna atrata* and *Acanthocnemus nigricans* from predation by birds. Under this hypothesis, rapid colonization and improved navigation at an active fire via IR sensors evolved as a means for providing shelter during foraging, mating, and oviposition (Schmitz et al., 2015).

A complementary hypothesis to the ideas suggested by Schmitz et al. (2015) and Poulton (1915) is that egg-laying substrates are sterilized by the extreme heat of fire and provide a reproductive advantage for rapidly colonizing pyrophilic species (Bell et al., 2022). Under this view, recently burnt substrates (soil, cambium of host trees, ash, etc.) are comparatively devoid of pathogens, predators, and other biological agents that regularly kill eggs. Individuals of both sexes are attracted to fire, copulate, and oviposit directly in substrates that, in some cases, are very close to active hot spots (Kreiss et al., 2005, Schmitz et al., 2015). These sterilized substrates, in turn, are most suitable immediately after they have cooled to a sufficient temperature that is conducive to egg survival. Moreover, eggs laid in substrates that are warmer than ambient conditions might increase development time and thereby reduce the duration spent in this vulnerable life stage. These substrates are only suitable for a short period of time because they are rapidly colonized by other organisms that compete for oviposition sites or contribute directly to egg mortality (Wikars and Schimmel, 2001, Bell et al. 2022). This hypothesis is consistent with various biological aspects of pyrophilic species discussed at length in this review (i.e., behaviour, physiology, and habitat-specificity). It is also consistent with the apparent association of many pyrophilic insects with pyrophilic fungi that form reproductive sporocarps only after wildfire, although consideration of pyrophilic fungi and their co-evolution with pyrophilic insects is beyond the scope of this review (but see Wikars, 1997, 2001, Raudabaugh et al., 2020).

Fire-induced reproductive behaviour and the potential adaptive benefits of pyrophily suggests that this strategy may have evolved as a form of reproductive synchrony. Reproductive synchrony refers to the temporal clustering of reproductive events (Riehl, 2018) and is thought to have evolved as an anti-predator response or as a means of coordinating reproduction with seasonal resource abundance (Rutberg, 1987, Ims, 1990). Indeed, the extended phenology and more evenly spread seasonal activity of pyrophilic species, including *Melanophila* spp., *Microsania* spp., *Sericoda* spp., *Merimna atrata*, and *Henotic serratus*, may be an adaptive strategy for dealing with the temporally unpredictable forest fires (Burke, 1919, Qvick, 1986, Lindroth, 1992, Wikars, 1997). In this case, the unpredictable habitat has given rise to adaptations that allow pyrophilic species to quickly colonize the fire, including improved olfactory and dispersal capabilities (e.g., Paarmann, 1966, Wikars, 1997, Schütz, 1999). Rapid colonization of the burn environment, in turn, provides reproductive trade-offs through an abundance of sterilized oviposition sites and reductions in egg-predation (Bell et al., 2022). These reproductive advantages wane over time as the post-burn environment regenerates and is colonized by other species, thus explaining the tendency for pyrophilic insects to emigrate from burns shortly after fire (Schmitz et al., 2015, Koivula et al., 2006).

7. Conservation of pyrophilic insects and future directions

Fire suppression and human-induced climate warming continue to alter natural fire regimes (Moritz et al., 2012, Wang et al., 2017, Hanes

et al., 2019). In Fennoscandia, for example, where suppression efforts have virtually eliminated naturally occurring fire, populations of many forest species have declined (Koivula and Vanha-Majamaa, 2020). Although disentangling the ultimate causes of these declines is challenging (e.g., removal of deadwood, loss of fire and heterogeneity in stand-age, etc.), it seems likely that fire suppression contributes to habitat loss and fragmentation for many pyrophilic species (Kouki et al., 2012, Ranius et al., 2014). Fossil evidence of pyrophilic species in areas where they are now extirpated, for example, suggests that some pyrophilic species were once widespread across much of Europe and likely declined due to human-induced changes in fire regimes (Lindroth, 1992, Whitehouse, 2000, Olsson and Lemdahl, 2009). Although climate warming and the associated increases in fire activity suggest that future availability of post-burn habitats will increase in many areas (Flannigan et al., 2001, Moritz et al., 2012, Wang et al., 2017, Hanes et al., 2019), little is known about how changes in the individual components of fire regimes (i.e., size, intensity, severity, frequency of fire) will impact population dynamics of pyrophilic insects.

Ongoing changes in fire behaviour and incomplete knowledge of their natural history make it difficult to assess the long-term extinction risk of pyrophilic species. One approach that requires only minimal information involves characterizing the rarity of species based on local abundance, habitat breadth, and geographic distribution (Rabinowitz, 1981). In the case of pyrophilic insects, many are considered rare due to their narrow niche and reliance on the post-burn environment (Falk and Crossley, 2005, Heikkala et al., 2017), but they are comparatively abundant and geographically widespread where these habitats occur (Wikars, 1997). A recent assessment of extinction risk associated with these aspects of rarity showed that reductions in geographic range led to pronounced increases in long-term extinction risk (Harnik et al., 2012). Given the impacts of fire suppression and associated changes in the spatial extent of fire over the last century (Cumming 2005, Campos-Ruiz et al., 2018), there is a growing need to better understand the spatial dynamics (i.e., metapopulations) and how these changes impact pyrophilic insects.

8. Conclusion

Burnt habitats are colonized by pyrophilic and non-pyrophilic species alike; however, characterizing a species' association with fire (and to what extent they are dependent on it) is complicated by the varying approaches to defining pyrophily in the literature. The analysis conducted for this review shows that two of the three commonly used approaches do not reliably distinguish between disturbance-adapted and pyrophilic species. Although pyrophilic species exhibit a strong attraction to fire and tend to be much more abundant in burnt environments than unburnt habitats, evidence of fire-specific adaptations are the best sole indicator of pyrophily as they reflect co-evolution with fire and specialization for exploiting burnt habitats. As such, future studies should consider the term pyrophily as synonymous with long-term dependence on fire and avoid classifying disturbance-adapted species as pyrophilic or "fire-favored," as many of these species respond to a wide range of perturbances that do not accommodate true pyrophiles. Management practices seeking to emulate the effects of fire through natural-disturbance-based harvesting may provide the necessary habitat (i.e., deadwood) for many disturbance-adapted species; however, without the use of prescribed burning, these practices are unlikely to conserve true pyrophiles.

Observations of pyrophilic behaviour at active fires and physiological studies of pyrophilic adaptations (i.e., IR sensors) suggest that the pyrophilic mode of life evolved as means for exploiting reproductive advantages in the post-burn environment. Active fires are colonized quickly, likely serving as a meeting place for both sexes, and copulation often occurs near hot spots or open flame. Some pyrophilic species also demonstrate a preference for ovipositing in burnt substrates, possibly as a means of increasing reproductive output in heat-sterilized substrates

that contain fewer competitors, egg predators, and other pathogens that contribute to egg mortality. The fact that these substrates are also quickly colonized by other organisms soon after the fire is extinguished serves as a possible explanation for the various adaptations among pyrophilic insects that facilitate rapid colonization of the burn. Furthermore, the tendency for some pyrophilic species to oviposit exclusively in burnt substrates may also provide clues for locating the unknown larval habitat of some pyrophilic Diptera (i.e., *Microsania*).

Much of our understanding of pyrophilic insects stems from studies of individual taxa and would benefit from a more holistic approach that considers the entire pyrophilic insect community (Fig. 2). Although the unpredictable occurrence of forest fires presents logistical challenges to studying pyrophilic species, the most valuable insights are likely to come from studies carried out immediately after fire, possibly with the assistance of local fire management authorities (e.g., Schmitz et al., 2015). Given their reliance on the post-burn environment, the highly disjunct and unpredictable occurrence of this habitat, and the need to emigrate from burns once they become unsuitable, studies focusing on the spatial dynamics of pyrophilic insect populations (e.g., Ranius et al., 2014) are sorely needed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have uploaded the data and code as Supplemental Material.

Acknowledgements

This research was supported by RBC's Tech for Nature grant awarded to Troutreach Saskatchewan, the Malcolm A. Ramsay Memorial Award, Natural Sciences and Engineering Research Council of Canada's (NSERC) Postgraduate Doctoral Scholarship (CGS D) and the Saskatchewan Ministry of Advanced Education's Queen Elizabeth II Centennial Aboriginal Scholarship awarded to the author.

I wish to extend my sincere thanks to K. Calladine, H. Schmitz, E. Hedlin, J. Rueggsegger, and my PhD committee members I. Phillips, D. Wardle, A. Davis, C. Laroque, and R. McIntosh for insightful discussion that improved the manuscript; J. Hammond, T. Cobb, M. Koivula, and N. Holliday for sharing data used in the meta-analysis; H. Schmitz for use of the IR sensor images he provided for Fig. 4; and S. Srayko, S. Paterson, K. Calladine, B. White for providing helpful comments on earlier drafts of the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120629>.

References

- Alexander, K.N.A., 2002. The invertebrates of living and decaying timber in Britain & Ireland – a provisional annotated checklist. English Nature Research Reports No. 647.
- Altner, H., Loftus, R., 1985. Ultrastructure and function of insect thermo- and hygroreceptors. *Annu. Rev. Entomol.* 30 (1), 273–295.
- Arno, S.F., Allison-Bunnell, S., 2002. Flames in our forest: disaster or renewal? Island Press, 2002. 227pp.
- Atkins, M.D., 1961. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae): III flight capacity. *Can. Entomol.* 93 (6), 467–474.
- Bell, A.J., Phillips, I.D., Nielsen, S.E., Spence, J.R., 2017. Boreal ground-beetle assemblages of the mainland and islands in Lac la Ronge, Saskatchewan, Canada. *Can. Entomol.* 149, 491–503.

- Bell, A.J., Calladine, K.S., Wardle, D.A., Phillips, I.D., 2022. Rapid colonization of the post-burn environment improves egg survival in pyrophilic ground beetles. *Ecosphere* 13 (8), e4213.
- Borowski, J., Gutowski, J.M., Slawski, M., Sućko, K., Zub, K., 2018. *Stephanopachys linearis* (Kugelann, 1972) (Coleoptera, Bostrichidae) in Poland. *Nature Conserv.* 27, 75–84.
- Boucher, J., 2010. Impacts de la coupe de recupération après feu sur les Coléoptères associés aux brûlis en forêt boréale: une dynamique temporelle. University of Quebec at Chicoutimi, Canada. M. Sc. thesis.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J. E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J., 2009. Fire in the Earth system. *Science* 324 (5926), 481–484.
- Buddle, C.M., Spence, J.R., Langor, D.W., 2000. Succession of boreal forest spiders assemblages following wildfire and harvesting. *Ecography* 23, 424–436.
- Burakowski, B., 1986. The life-cycle and food preference of *Agonum quadri-punctatum* (De Geer). – In: Den Boer, P.J., Grün, Szyszko, J. (eds.), *Feeding behaviour and accessibility of food for carabid beetles*: 35–39. Warsaw Agricultural University Press.
- Burke, H.E., 1919. Biological notes on some flatheaded barkborers of the genus *Melanophila*. *J. Econ. Entomol.* 12, 105–108.
- Bryers, J.A., 2000. Wind-aided dispersal of simulated bark beetles flying through forests. *Ecol. Model.* 125, 231–243.
- Cadorette-Breton, Y., 2014. Étude des facteurs régissant la répartition des longicornes (Coleoptera: Cerambycidae) dans les arbres tués par le feu en forêt boréale. Université Laval, Canada. M. Sc. thesis.
- Campos-Ruiz, R., Parisien, M.-A., Flannigan, M.D., 2018. Temporal patterns of wildfire activity in areas of contrasting human influence in the Canadian boreal forest. *Forests* 9, 159.
- Champion, G.C., 1918. A note on the habits of a *Melanophila* (Buprestidae) and other Indian Coleoptera. *Entomologist's Monthly Magazine* 54, 199–200.
- Chandler, P.J., 1978. Some dipterous opportunists at Windsor Forest, Berks: the attraction for flies of bonfires, wood ash and freshly cut logs. *Entomologist's Gazette* 29, 253–257.
- Chandler, P.J., 1992. Some further records of *Astiosoma rufifrons* Duda (Diptera: Asteiidae). *Br. J. Entomol. Nat. History* 5, 14.
- Chandler, P.J., 2001. The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomol. Scand.* 6, 1–276.
- Chase, K.D., Kelly, D., Liebhold, A.M., Bader, M.-K.-F., Brockerhoff, E.G., 2017. Long-distance dispersal of non-native pine bark beetles from host resources. *Ecol. Entomol.* 42, 173–183.
- Cobb, T.P., Langor, D.W., Spence, J.R., 2007. Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Can. J. For. Res.* 37, 1310–1323.
- Collart, A., 1958. Observations sur les *Microsania* (Dipt., Platypezidae). *Bulletin & Annales de la Société Entomologique de Belgique*.
- Cumming, S.G., 2005. Effective fire suppression in boreal forests. *Can. J. For. Res.* 35, 772–786.
- Davis, A.K., Holden, M.T., 2015. Measuring intraspecific variation in flight-related morphology of monarch butterflies (*Danaus plexippus*): which sex has the best flying gear? *Journal of Insects* 2015: Article ID 591705.
- DeLong, S.C., Tanner, D., 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiv. Conserv.* 5, 1191–1205.
- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russel-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J., York, A., 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biol. Conserv.* 143, 1928–1939.
- Eßinger, T.M., Becker, B., Sauerwald, T., Kohl, C.-D., Paczkowski, S., Schütz, S., 2010. Volatile gas sensors for large-scale drying of wood, in: *Sensoren und Messsysteme* 2010, Nürnberg, Germany, 2010.
- Edwards, F.W., 1934. *Microsania pectinipennis* Mg. (Diptera, Platypezidae) attracted to bonfire smoke. *J. Soc. Br. Entomol.* 1, 31–32.
- Evans, W.G., 1962. Notes on the biology and dispersal of *Melanophila*. *The Pan-Pacific Entomol.* 38, 59–61.
- Evans, W.G., 1964. Infra-red receptors in *Melanophila acuminata* DeGeer. *Nature* 202, 211.
- Evans, W.G., 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* de Geer (Buprestidae, Coleoptera). *Ecology* 47, 1061–1065.
- Evans, W.G., 1972. The attraction of insects to forest fires. Tall Timbers Conference on Ecological Animal Control by Habitat Management 3: 115–127.
- Evans, W.G., 2010. Reproductive role of infrared radiation sensors of *Melanophila acuminata* (Coleoptera: Buprestidae) at forest fires. *Ann. Entomol. Soc. Am.* 103, 823–826.
- Falk, S.J., Crossley, R., 2005. A review of the scarce and threatened flies of Great Britain. Part 3: Empidoidea. *Species Status No.* 3, JNCC, Peterborough, ISSN 1473-0154.
- Flannigan, M.D., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., Bergeron, Y., 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model-regional climate model simulations. *Can. J. For. Res.* 31, 854–864.
- Fredriksson, E., Pettersson, R.M., Naalisvaara, J., Löfroth, T., 2020. Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden. *Ecol. Processes* 9, 44.
- Ghoneim, A.F., Zhang, X., Knio, O., Baum, H.R., Rehm, R.G., 1993. Dispersion and deposition of smoke plumes generated by massive fires. *J. Hazard. Mater.* 33, 275–293.
- Glasspool, I.J., Edwards, D., Axe, L., 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology* 32, 381–383.
- Goodman, K., McCravy, K.W., 2008. Pyrophilous insects. In: Capinera, J.L. (Ed.), *Encyclopedia of Entomology*. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-6359-6_3272.
- Gordon, M., Lumley, T., 2021. forestplot: advanced forest plot using 'grid' Graphics. R package version 2, 1. <https://CRAN.R-project.org/package=forestplot>.
- Government of Canada 2022 – accessed here <https://www.nrcan.gc.ca/our-natural-resources/forests-forestry/wildland-fires-insects-disturban/forest-fires/13143>. Accessed 13/04/2022.
- Hadley, W., François, R., Lionel, H., Müller, K., 2021. dplyr: A grammar of data manipulation. R package version 1, 7. <https://CRAN.R-project.org/package=dplyr>.
- Hägglund, R., Hekkala, A.-M., Hjäältén, J., Tolvanen, A., 2015. Positive effects of ecological restoration on rare and threatened flat bugs (Heteroptera: Aradidae). *J. Insect Conserv.* 19, 1089–1099.
- Hanes, C.C., Wang, X., Jain, P., Parisien, M.-A., Little, J.M., Flannigan, M.D., 2019. Fire regime changes in Canada over the last half century. *Can. J. For. Res.* 49, 256–269.
- Harnik, P.G., Simpson, C., Payne, J.L., 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proc. Roy. Soc. B* 279, 4969–4976.
- Heikkala, O., Martikainen, P., Kouki, J., 2017. Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat bugs. *Insect Conserv. Div.* 10, 32–41.
- Hekkala, A.-M., Päätaalo, M.-L., Tarvainen, O., Tolvanen, A., 2015. Restoration of young forests in eastern Finland: benefits for saproxylic beetles (Coleoptera). *Restor. Ecol.* 22, 151–159.
- Hingley, M.R., 1971. The ascomycete fungus, *Daldinia concentrica* as a habitat for animals. *J. Anim. Ecol.* 40, 17–32.
- Hinz, M., Klein, A., Schmitz, A., Schmitz, H., 2018. The impact of infrared radiation in flight control in the Australian “firebeetle” *Merimna atrata*. *PLoS ONE* 13, e0192865.
- Hjäältén, J., Gibb, H., Ball, J.P., 2010. How will low-intensity burning after clear-felling affect mid-boreal insect assemblages? *Basic Appl. Ecol.* 11, 363–372.
- Hjäältén, J., Hägglund, R., Löfroth, T., Roberge, J.-M., Dynesius, M., Olsson, J., 2017. Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. *Biodivers. Conserv.* 26, 1623–1640.
- Hoang, T., 2020. Adaptations of pyrophilous insects to burnt habitats: odor signals, infrared receptors, and behavior. University of Göttingen, Germany. PhD. thesis.
- Holliday, N.J., 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp.). *Can. Entomol.* 116, 919–992.
- Holliday, N.J., 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Can. Entomol.* 123, 1369–1389.
- Hunter Jr., M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* 65, 115–120.
- Hutto, R.L., 1995. Composition of bird communities following stand-replacing fires in northern rocky mountain (U.S.A.) conifer forests. *Conserv. Biol.* 9, 1041–1058.
- Hyvärinen, E., Kouki, J., Martikainen, P., Lappalainen, H., 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *For. Ecol. Manage.* 212, 315–322.
- Ims, R.A., 1990. The ecology and evolution of reproductive synchrony. *Trends Ecol. Evol.* 5, 135–140.
- Jackson, P.L., Straussfogel, D., Lindgren, B.S., Murphy, B., 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Can. J. For. Res.* 38, 2313–2327.
- Jactel, H., Gaillard, J., 1991. A preliminary study of the dispersal potential of *Ips sexdentatus* (Boern) (Col., Scolytidae) with an automatically recording flight mill. *J. Appl. Entomol.* 112, 138–145.
- Johannesson, H., Læssøe, T., Stenlid, J., 2000. Molecular and morphological investigation of *Daldinia* in northern Europe. *Mycol. Res.* 104, 275–280.
- Kelley, K., 2005. The effects of nonnormal distributions on confidence intervals around the standardized mean difference: bootstrap and parametric confidence intervals. *Educ. Psychol. Measur.* 65, 51–69.
- Kessel, E.L., 1947. American smoke flies (Microsania: Clythiidae). *The Wasmann Collector* 7, 23–30.
- Kessel, E.L., 1952. Another American smoke fly (Diptera: Empidoidea). *The Pan-Pacific Entomologist* 28, 56–58.
- Kessel, E.L., 1960. The response of *Microsania* and *Hormopeza* to smoke. *Pan-Pacific Entomol.* 36, 67–68.
- Klocke, D., Schmitz, A., Schmitz, H., 2009. Native flies attracted to brushfires. *Science Division Information Sheet* 15/2009. Department of Environment and Conservation, Perth.
- Klocke, D., Schmitz, A., Schmitz, H., 2011. Fire-adaptation in *Hypocerides nearcticus* Borgmeier and *Anabarhynchus hyalipennis hyalipennis* Marquart and new notes about the Australian “smoke fly” *Microsania australis* Collart (Diptera: Phoridae, Therevidae, and Platypezidae). *Open Entomol. J.* 5, 10–14.
- Klocke, D., Schmitz, H., 2012. Material properties of photomechanical infrared receptors in pyrophilous *Melanophila* beetles and *Aradus* bugs. *Acta Biomater.* 8, 3392–3399.
- Koivula, M., Cobb, T., Déchène, A.D., Jacobs, J., Spence, J.R., 2006. Responses of two *Sericoda* Kirby, 1837 (Coleoptera: Carabidae) species to forest harvesting, wildfire, and burn severity. *Entomologica Fennica* 17, 315–324.
- Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. *Ecol. Processes* 9, 1–22.
- Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., Similä, M., 2012. Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Divers. Distrib.* 18, 348–355.

- Kreiss, E.-J., Schmitz, A., Schmitz, H., 2005. Morphology of the prothoracic discs and associated sensilla of *Acanthocnemus nigricans* (Coleoptera: Acanthocnemidae). *Arthropod Struct. Dev.* 34, 419–428.
- Kreiss, E., Schmitz, H., Gebhardt, M., 2007. Electrophysiological characterisation of the infrared organ of the Australian “little ash beetle” *Acanthocnemus nigricans* (Coleoptera, Acanthocnemidae). *J. Comp. Physiol. A* 193, 729–739.
- Larochelle, A., Larivière, M.-C., 2003. A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft Publishers, Bulgaria, p. 584.
- Lee, S.-I., Spence, J.R., Langor, D.W., Pinzon, J., 2015. Retention patch size and conservation of saproxylic beetles in boreal white spruce stands. *For. Ecol. Manage.* 358, 98–107.
- Lindemayer, D.B., Franklin, J.F., Löhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygesen, A., Volney, A.W., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* 5, 421–431.
- Lindroth, C. H., 1969. The ground-beetles of Canada and Alaska. *Opuscula Entomologica Supplement* 20, 24, 26, 29, 33, 34, 35: 1-1192.
- Lindroth, C.H., 1972. Changes in the Fennoscandian ground-beetle fauna (Coleoptera, Carabidae) during the twentieth century. *Ann. Zool. Fenn.* 9, 49–64.
- Lindroth, C.H., 1992. Ground beetles (Carabidae) of Fennoscandia: a zoogeographic study. Part 1. Specific knowledge regarding the species. Amerind Publishing, New Delhi.
- Linsley, E.G., 1933. Some observations on the swarming of *Melanophila*. *Pan-Pacific Entomol.* 9, 138.
- Linsley, E.G., 1943. Attraction of *Melanophila* beetles by fire and smoke. *J. Econ. Entomol.* 36, 341–342.
- Linsley, E.G., Hurd, P.D., 1957. *Melanophila* beetles at cement plants in southern California (Coleoptera, Buprestidae). *Coleopterists' Bulletin* 11, 9–11.
- Lundberg, S., 1984. The beetle fauna of burnt forest in Sweden. *Entomol. tidskrift* 105, 129–141.
- Mainz, T., Schmitz, A., Schmitz, H., 2004. Variation in the number and differentiation of the abdominal infrared receptors in the Australian ‘fire-beetle’ *Merimna atrata* (Coleoptera, Buprestidae). *Arthropod Struct. Dev.* 33, 419–430.
- Martin, R.E., Sapsis, D.B., 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Proceedings of the Symposium on Biodiversity in Northwestern California. Wildland Resource Centre, University of California, Berkeley.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* 9, 223–260.
- Melander, A.L., 1922. *Microsania*, a genus of Platypyzidae. *Psyche* 29, 43–48.
- Middlekauff, W.W., 1964. Notes and description of the previously unknown male of *Syntaxis libocedrii*. *Pan-Pacific Entomol.* 40, 255–258.
- Milberg, P., Bergman, K.-O., Norman, H., Pettersson, R.B., Westerberg, L., Wikars, L.-O., Jansson, N., 2015. A burning desire for smoke? Sampling insects favoured by forest fire in the absence of fire. *J. Insect Conserv.* 19, 55–65.
- Moritz, M.A., Parisien, M.-A., Battlori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J., Hayhoe, K., 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3, 49.
- Morley, C., 1938. The true smoke flies. *Trans. Suffolk Naturalists' Society* 1, 78.
- Muona, J., Rutanen, I., 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Ann. Zool. Fenn.* 31, 109–121.
- Nappi, A., Drapeau, P., Savard, J.-P.-L., 2004. Salvage logging after wildfire in the boreal forest: is it becoming a hot issue for wildlife? *The Forestry Chronicle* 80, 67–74.
- Nitschke, C.R., 2005. Does forest harvesting emulate fire disturbance? A comparison of effects on selected attributes in coniferous-dominated headwater systems. *For. Ecol. Manage.* 214, 305–319.
- Norberg, U.M., 1990. *Vertebrate flight*. Springer-Verlag, Berlin.
- Norberg, U.M., 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* 9, 48–54.
- Olsson, F., Lemdahl, G., 2009. A continuous Holocene beetle record from the site Stavsåkra, southern Sweden: implications for the last 10 600 years of forest and land use history. *J. Quat. Sci.* 24, 612–626.
- Paarmann, W., 1966. Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*Pterostichus angustatus* Dft. und *Pterostichus oblongopunctatus* F.) an ihre verschiedenen Lebensräume. *Zeitschrift für wissenschaftliche Zoologie. Abteilung A* 174, 83–176.
- Paczkowski, S., Paczkowska, M., Dippel, S., Schulze, N., Schütz, S., Sauerwald, T., Weiß, A., Bauer, M., Gottschald, J., Kohl, C.-D., 2013. The olfaction of a fire beetle leads to new concepts for early fire warning systems. *Sens. Actuators, B* 183, 273–282.
- Paczkowski, S., Sauerwald, T., Weiß, A., Bauer, M., Kohl, D. and Schütz, S., 2011. Biomimetic gas sensors for large-scale drying of wood particles, In: SPIE Smart Structures and Materials+ Nondestructive Evaluation and Health Monitoring. International Society for Optics and Photonics, pp. 797505–8.
- Pausus, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. *Bioscience* 59, 593–601.
- Poulton, E.B., 1915. The habits of the Australian buprestid “fire-beetle” *Merimna atrata*, Lap. et Gory. *Transactions of the Entomological Society of London*, pt. 1, proc., iii-iv.
- Pinzon, J., Spence, J.R., Langor, D.W., 2013. Effects of prescribed burning and harvesting on ground-dwelling spiders in the Canadian boreal mixedwood forest. *Biodiv. Conserv.* 22, 1513–1536.
- Pratt, L., Urquhart, I., 1994. The last great forest. NeWest Press, Edmonton, Alberta, Canada.
- Qvick, U., 1986. The distribution, flight-periods and occurrences of Swedish flat-footed flies. (In Swedish with English summary). *Entomologisk Tidskrift* 107, 11–16.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.
- Rabinowitz, D., 1981. Seven forms of rarity. In: Synges, H. (Ed.), *The biological aspects of rare plant conservation*. John Wiley & Sons Ltd., New York, NY, pp. 205–217.
- Ranius, T., Bohman, P., Hedgren, O., Wikars, L.-O., Caruso, A., 2014. Metapopulation dynamics of a beetle species confined to burned forest sites in a managed forest region. *Ecography* 37, 797–804.
- Raudabaugh, D.B., Matheny, P.B., Hughes, K.W., Iturriaga, T., Sargent, M., Miller, A.N., 2020. Where are they hiding? Testing the body snatchers hypothesis in pyrophilous fungi. *Fungal Ecol.* 43, 100870.
- Ricksecker, L.E., 1885. Habits of some California beetles. *Entomol. Am.* 1, 96–98.
- Riehl, C., 2018. Reproductive Synchrony. In: Vonk, J., Shackelford, T. (Eds.), *Encyclopedia of Animal Cognition and Behavior*. Springer, Cham. https://doi.org/10.1007/978-3-319-47829-6_2010-1.
- Russell, H.M., 1960. *Microsania pectinipennis* (Mg.) in Yorkshire. *Entomol. Monthly Mag.* 96, 100.
- Rutberg, A.T., 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am. Nat.* 130, 692–710.
- Saint-Germain, M., Drapeau, P., Buddle, C.M., 2008. Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. *Divers. Distrib.* 14, 713–720.
- Schmitz, A., Gebhardt, M., Schmitz, H., 2008. Microfluidic photomechanic infrared receptors in a pyrophilous flat bug. *Naturwissenschaften* 95, 455–460.
- Schmitz, A., Schätzel, H., Schmitz, H., 2010. Distribution and functional morphology of photomechanic infrared sensilla in flat bugs of the genus *Aradus* (Heteroptera, Aradidae). *Arthropod Struct. Dev.* 39, 17–25.
- Schmitz, A., Schneider, E.S., Schmitz, H., 2015. Behaviour of the Australian ‘fire-beetle’ *Merimna atrata* (Coleoptera: Buprestidae) on burnt areas after bushfires. *Rec. Western Aust. Museum* 30, 1–11.
- Schmitz, A., Schmitz, H., 2021. Sensory equipment and adaptations to the fire habitat of the antennae of the Australian ‘fire beetle’ *Merimna atrata* (Coleoptera; Buprestidae). *Zoomorphology* 140, 487–504.
- Schmitz, H., Bleckmann, H., Mürtz, M., 1997. Infrared detection in a beetle. *Nature* 386, 773–774.
- Schmitz, H., Bleckmann, H., 1997. Fine structure and physiology of the infrared receptors of beetles of the genus *Melanophila* (Coleoptera: Buprestidae). *Int. J. Insect Morphol. Embryol.* 26, 205–215.
- Schmitz, H., Bleckmann, H., 1998. The photomechanic infrared receptor for the detection of forest fires in the beetle *Melanophila acuminata* (Coleoptera: Buprestidae). *J. Comp. Physiol.* 182, 647–657.
- Schmitz, H., Schmitz, A., Bleckmann, H., 2000. A new type of infrared organ in the Australian “fire-beetle” *Merimna atrata* (Coleoptera: Buprestidae). *Naturwissenschaften* 87, 542–545.
- Schmitz, H., Schmitz, A., Bleckmann, H., 2001. Morphology of a thermosensitive multipolar neuron in the infrared organ of *Merimna atrata* (Coleoptera, Buprestidae). *Arthropod Struct. Dev.* 30, 99–111.
- Schmitz, H., Trenner, S., 2003. Electrophysiological characterization of the multipolar thermoreceptors in the “fire-beetle” *Merimna atrata* and comparison with the infrared sensilla of *Melanophila acuminata* (both Coleoptera, Buprestidae). *J. Comp. Physiol. A* 189, 715–722.
- Schmitz, H., Bousack, H., 2012. Modelling a historic oil-tanker fire allows an estimation of the sensitivity of the infrared receptors in pyrophilous *Melanophila* beetles. *PLoS ONE* 7, e37627.
- Schmitz, H., Schmitz, A., Schneider, E.S., 2016. Matched filter properties of infrared receptors used for fire and heat detection in insects. In: *The Ecology of Animal Senses: Matched Filtering for Economical Sensing*; Warrant, G.V.D.E.E., Ed.; Springer-Verlag, Berlin, Heidelberg, Germany.
- Schneider, E.S., Schmitz, H., 2013. Bimodal innervation of the infrared organ of *Merimna atrata* (Coleoptera, Buprestidae) by thermo- and mechanosensory units. *Arthropod Struct. Dev.* 42, 135–142.
- Schneider, E.S., Schmitz, H., 2014. Thermomechanical properties of the stimulus transducing cuticle in the infrared organ of *Merimna atrata* (Coleoptera, Buprestidae). *J. Morphol.* 275, 991–1003.
- Schneider, E.S., Schmitz, A., Schmitz, H., 2015. Concept of an active amplification mechanism in the infrared organ of pyrophilous *Melanophila* beetles. *Front. Physiol.* 6, 391.
- Scholtz, C.H., MacRae, T., 2016. *Melanophila unicolor* Gory, 1841 (Buprestidae), the furnace beetle, in southern Africa. *African Entomology* 24, 241–244.
- Schütz, S., Weissbecker, B., Hummel, H.E., Apel, K.-H., Schmitz, H., Bleckmann, H., 1999. Insect antenna as a smoke detector. *Nature* 398, 298–299.
- Severin, G., 1921. Notes sur le *Microsania stigmatalis* Zett. (Dipt.) *Bulletin & Annales de la Société Entomologique de Belgique* 3, 178–179.
- Sharp, W.E., 1918. *Melanophila acuminata* DeG in Berkshire. *Entomol. Monthly Mag.* 54, 244–245.
- Silge, J., Robinson, D., 2016. tidytext: text mining and analysis using tidy data principles in R. *J. Open Source Software* 1, 37. <https://doi.org/10.21105/joss.00037>.
- Sinclair, B.J., Cumming, J.M., 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* 1180, 1–172.
- Snoddy, E.L., Tippins, H.H., 1968. On the ecology of a smoke fly, *Microsania imperfecta*. *Ann. Entomol. Soc. Am.* 61, 1200–1201.
- Stocks, B.J., Martell, D.L., 2016. Forest fire management expenditures in Canada: 1970–2013. *Forestry Chronicle* 92, 298–306.
- Sundin, F., 2014. Occurrence of insects in relation to short term fire history. Linköping University, Sweden. M. Sc. thesis.

- Tepper, J.G.O., 1887. Common native insects of south Australia. A popular guide to south Australian entomology. Part 1. Coleoptera or Beetles. E.S. Wigg & Son, Adelaide, pp. 1–46.
- Tkoč, M., Tóthová, A., Ståhls, G., Chandler, P.J., Vaňhara, J., 2017. Molecular phylogeny of flat-footed flies (Diptera: Platypezidae): main clades supported by new morphological evidence. *Zool. Scr.* 46, 429–444.
- Van Dyke, E.C., 1926. Buprestid swarming. *The Pan-Pacific Entomologist* 3, 41.
- Van Dyke, E.C., 1928. *Melanophila consputa* LeC. *The Pan-Pacific Entomol.* 4, 113.
- Vondran, T., Apel, K.-H., Schmitz, H., 1995. The infrared receptors of *Melanophila acuminata* DeGeer (Coleoptera: Buprestidae): ultrastructural study of a unique insect thermoreceptor and its possible descent from a hair mechanoreceptor. *Tissue Cell* 27, 645–658.
- Wang, X., Parisien, M.-A., Taylor, S.W., Candau, J.-N., Stralberg, D., Marshall, G.A., Little, J.M., Flannigan, M.D., 2017. Projected changes in daily fire spread across Canada over the next century. *Environ. Res. Lett.* 12, 025005.
- Whitehouse, N.J., 2000. Forest fires and insects: palaeoentomological research from a subfossil burnt forest. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164, 231–246.
- Wickman, B.E., 1964. Attack habits of *Melanophila consputa* on fire-killed pines. *Pan-Pacific Entomol.* 40, 183–186.
- Wickman, B.E., 1967. Life history of the incense-cedar wood wasp, *Syntexis libocedrii*, (Hymenoptera: Syntexidae). *Ann. Entomol. Soc. Am.* 60, 1291–1295.
- Wikars, L.-O., 1995. Clear-cutting before burning prevents establishment of fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Ann. Zool. Fenn.* 32, 375–384.
- Wikars, L.-O., 1997. Effects of forest fire and the ecology of fire-adapted insects. *Acta University Uppsala Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 272: p. 35.
- Wikars, L.-O., Schimmel, J., 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *For. Ecol. Manage.* 141, 189–200.
- Wikars, L.-O., 2001. The wood-decaying fungus *Daldinia loculata* (Xylariaceae) as an indicator of fire-dependent insects. *Ecol. Bull.* 49, 263–268.
- Wikars, L.-O., 2006. Åtgärdsprogram för bevarande av brandinsekter i boreal skog. Naturvårdsverket Rapport 5610, 78 pp. <http://www.naturvardsverket.se/Om-Naturvardsverket/Publikationer/ISBN/5600/91-620-5610-7/>.