



Facing the flames: insect responses to megafires and changing fire regimes

Haley E Dole¹, Santiago Villamarin-Cortez^{1,2} and Lora A Richards¹

The rise of megafires and extreme fire behaviors poses a significant threat to insect populations, affecting their survival and postfire recolonization. Megafires threaten the entire insect communities by changing fire regimes and habitats. These fires are now burning non-fire-prone ecosystems, endangering non-fire-adapted insects and habitats. While implementing prescribed burn programs can reduce the chances of megafires from developing, some megafires will be unpreventable. Land managers can mitigate the fire impacts by creating refugia and promoting heterogeneity in burn severity through fire control measures. Last, these post-megafire landscapes can provide an opportunity to restore historical fire regimes through subsequent prescribed burn management. This will revitalize ecosystems, benefit insects, and reduce the likelihood of future megafires and subsequent insect loss.

Addresses

¹ University of Nevada–Reno, 1664 North Virginia Street, Reno, NV 89557, USA

² Universidad Central del Ecuador, Facultad de Ciencias Biológicas, Dirección de Posgrado, Numa Pompilio Llona y Yaguachi, Quito, Ecuador

Corresponding author: Dole, Haley E (hdole@unr.edu)

Current Opinion in Insect Science 2023, **60**:101129

This review comes from a themed issue on Global change biology

Edited by **Matthew Forister, Angela Smilanich, Lee Dyer and Zach Gompert**

For complete overview about the section, refer “[Global change Biology \(October 2023\)](#)”

Available online 5 October 2023

<https://doi.org/10.1016/j.cois.2023.101129>

2214–5745/© 2023 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

Recent megafires have reached unprecedented sizes, consuming millions of hectares rapidly with high intensity [1], penetrating areas of fire refugia [2], and leaving large contiguous patches of severely burned land [3]. Megafires are wildfires that burn over 10 000 ha [4•]. Historically, megafires were a rare phenomenon occurring within fire-prone

ecosystems, but recent global changes in climate, land use, fire suppression strategies, and the spread of invasive species have led to an increase in megafire frequency, including in non-fire-adapted ecosystems such as tundra [1,5,6]. The increasing frequency of megafires imposes an emerging threat for the exceptionally diverse group, insects. These more frequent and intense megafires have placed non-fire-adapted insects and their habitats at risk [7] and alter the fire experiences for fire-adapted insects compared with historical fire regimes.

Megafires and accompanying abnormal fire behaviors disrupt historical insect responses to fire. Many insects benefit from and depend on wildfires or prescribed burns to maintain their habitats, including pollinators, herbivores, and decomposers [8–10]. However, these positive effects of fire can be reversed when fire regimes are altered [7]. With such drastic alterations of natural fire regimes, extinctions and changes in insect communities and their ecosystem services (i.e. decomposition, pollination, nutrient cycling, and soil respiration) can be expected. Recent reviews and meta-analyses summarize the specific impacts of fire on insects [8,11•,12], however, research on the effects of megafires is an emerging field. Here, we review studies documenting insect responses to megafires and discuss factors by which megafires deviate from historical fire regimes to threaten insects. We also address knowledge gaps in our understanding of how megafires affect insects and propose needs for conservation.

Insect survival

The massive extent of megafires and their associated extreme fire behaviors prevent insects from escaping. To survive a megafire, insects must travel greater distances, for longer periods, and often at increased speeds compared with fires of historical regimes. Insects with limited dispersal ability are likely to be caught in the flames, while those able to disperse risk moving beyond their habitat range. Additionally, exposure to smoke of large fires can impair insect flight ability such as by reducing butterfly flight distance and speed [13] or by causing insect disorientation [14•]. Furthermore, the scale of megafires alters fire behavior, generating powerful updrafts and firestorms [15] that impede escape. Such fire-weather effects pushed insects out to sea during an Australian megafire, resulting in masses of dead insects

washing up on beaches [16•]. As megafires become more frequent, we can anticipate significant insect losses due to their inability to escape and being forced outside their habitat ranges.

During fires, insects seek refugia, such as unburnt patches of vegetation, logs, duff, or by climbing up trees [17]. Refugia play an important role in increasing insect diversity postfire [18–20]. However, the increased fire severity, large contiguous burn areas, and increased crown fires in megafires result in less refugia [3,21,22]. Not only are there less refugia, but those that remain are highly degraded in quality [23], leading to decreased insect diversity [22]. Intense fire weather can also overrun topographic controls, making refugia less predictable [24], thus, historically safe places no longer offer protection. The consequences of lost refugia will be long-lasting. Nine years following a European–Russia megafire, insects had recovered in areas with low-intensity surface burns but remain affected in areas with high-intensity crown fires [25].

Research following the recent Australian megafires document catastrophic effects on insect survival. In a single season, 30.38–39.8 million ha of vegetation burned [26]. The fires spread rapidly at high intensity, leaving little unburned and infiltrating areas typical of fire refugia and neighboring non-fire-prone ecosystems such as rainforest [27]. In 26% of the burned area, it was estimated that 240 trillion arthropods died [26]. At this scale, the entire host plant populations and habitats were destroyed, causing the extirpation and extinction of an estimated 50 host plant dependent insects, including fire-adapted species [28•,29]. The fires also resulted in 29 bee species becoming eligible for International Union for Conservation of Nature (IUCN) listing [30]. Given that only 30% of Australian invertebrates are described [31], the true extent of the impact was likely far greater than documented.

Similar results have been observed following other megafires. In Borneo between 1997 and 1998, over 5 million ha of forest burned, causing a major decline in native butterfly species richness, and shifting the butterfly community from specialist-rich to one dominated by large-winged generalists postfire. These more mobile species had an advantage in their ability to travel greater distances and utilize a broader range of host plants [32]. Even after four years, only 43% of the prefire species were found to persist postfire [33]. Over 100 butterfly species were temporarily extirpated, with these species tending to be restricted in range, smaller, specialized, and less abundant prefire [34]. Likewise, 16 months after a Brazilian megafire, eight dung beetle species were temporarily extirpated, with fire-sensitive species replaced by more tolerant ones [35].

Postfire recovery, insects, and ecosystems

Megafires can decimate an insect's entire habitat and geographic extent [36••] destabilizing numerous insect populations [28•]. Following the 2019–2020 Australian megafires, it was estimated that ~400 invertebrate species had their whole geographic range burned, and another ~400 had over half their range burned [36••]. Insects surviving megafires face immediate resource scarcity, likely causing further die-off from starvation and exposure [9]. Late successional species are especially vulnerable to this postfire die-off, as it can take decades for their habitat to recover (e.g. buildup of dead wood, leaf litter, or old-growth plant architectures) [37]. Columbian dung beetles, which decline in diversity following fire, demonstrate the vulnerability of late-succession groups to fire [38]. Last, following megafires, recolonization will be slower due to fewer and smaller populations available to source recovery [39].

Post-megafire landscapes have fewer intact habitat patches, which are critical for the recovery of individual species and ecosystems [19,23,40,41]. Since insect recolonization typically originates from the unburned perimeter moving inward [22,42,43], larger burned areas and reduced intact habitat surrounding post-megafire landscapes prolongs recolonization. The ability of insects to detect a suitable habitat is limited by distance, and without habitat cues to guide insects, random searching behavior for postfire habitat can increase mortality due to predation and energy loss [44]. Additionally, longer distances to isolated habitats reduce pollinator richness and floral visitation rates, negatively impacting the reproduction of surviving vegetation [45], further disrupting ecosystem recovery. Furthermore, large intensively burned areas create high-contrast boundaries between habitat patches [44] that may slow or discourage insect dispersal [46,47]. Megafires also increase the risk of recolonization failure. Marschalek et al. [48] found only two cases of a rare butterfly's recolonization six years after two megafires in California coastal sage brush. Burn size has been found to decrease the recolonization potential of some cockroaches, further delaying ecosystem recovery by limiting their contribution to decomposition [43].

Losses of insect species from fire may weaken ecosystem integrity [49] and cause changes to communities that disrupt ecosystem functioning. A megafire in Portugal led to a loss of mountain shrubland community resilience, where nocturnal moth pollen transport networks became less complex and robust, and moth abundance, species richness, and total pollen transport decreased despite an increased flowering [50]. Similarly, following a megafire in California, ecosystem network stability decreased for three years post fire where the fire was most severe [51].

Megafire duration and fire season expansion

Many insects are only fire-adapted within specific life stages synchronized with historical fire seasons, such as the *Atala* hair streak, which pupates belowground during the fire season [52]. As megafires burn longer, often extending beyond the typical fire season, insects are experiencing fires during vulnerable life stages, which can have devastating effects. For instance, pre-season fires that occurred before a skipper butterfly was in the mobile adult stage led to the skipper's local extirpation [37]. Species with highly synchronized phenology or short generation times are particularly vulnerable to megafires occurring outside of historic fire seasons. Changes in the timing of fires can reshape the entire insect communities. After prescribed burns in Texas grassland and prairie during the summer, there was a 170% increase in arthropods with a higher portion of predaceous and herbivorous groups compared with prescribed burns in the winter [53]. This shift in insect communities may be partly due to the effects of seasonal fire timing on resource availability. Historically, fires occur during the growing season, creating bare soil patches for ground-nesting bees. These important nesting resources are reduced with fire seasons expanding into the dormant season [54]. The seasonal timing and frequency of fires impacts the plant communities that support insect communities. Fires outside of the fire season can alter plant survival, reproduction [55], and diversity [56], which in turn impacts insect herbivores and pollinators. Last, megafires can reduce fire return intervals beyond plant thresholds, risking ecosystem collapse [2,57,58]. As increasing megafires alter fire regimes, vegetation transitions will result in insect habitat and host plant loss, coinciding with declines in insect diversity.

Effect on non-fire-prone insect communities

Intense megafires can extend into non-fire-prone ecosystems, such as wet sclerophyll forests, rainforests, and alpine complexes [2,59] posing risks to non-fire-adapted insects [7]. In these areas, fire avoidance behaviors may be weak or absent, resulting in poor fire detection and escape abilities [60]. Even in fire-prone systems, naive behaviors have been observed. Gerson and Kelsey [61] found that nocturnal pandora moths were attracted to the fire light at night and flew into the flames. Those disturbances or fire-naive individuals that survive, are likely to be more vulnerable to postfire risks, such as increased avian predation [60] or be unable to camouflage against charred landscapes [62]. Non-fire-prone insects may also exhibit maladaptive behaviors in post-fire environments. Social worker ant colonies are more vulnerable to attack as they are less likely to defend against threatening stimuli in recently burned habitats [63•]. Disturbance-sensitive insects may have more difficulty recolonizing. For example, after a disturbance

occurred in the wetland habitat of a *Batrachedra* species, the butterfly was unable to find host plants just 200 m away from its original, intact habitat. This disruption nearly led to the collapse of the plant–herbivore interaction [64]. Henry et al. [65] found that fires can have long legacies in non-fire-prone ecosystems, observing postfire differences in insect and mite species composition persisting 54+ years in fire-sensitive vegetation. Last, megafires can degrade and destroy non-fire-prone habitats, jeopardizing the entire insect communities. In the tundra, fires increase the risk of permafrost thaw melt, converting tundra to forest or shrublands [66], leading to the immigration of southern species north [67].

Effects beyond the fire

The impact of megafires extends beyond the flames, as smoke plumes pollute air quality and affect insect health and behavior. Smoke can reduce egg hatching, development, and survival in some species while increasing egg production and development in others [14•]. Smoke drifts have been observed to agitate hibernating monarch colonies and increase predation risk [68,69]. Anomalous sky polarization caused by smoke plumes can impair insect navigation and migration [70]. In addition to affecting survival and behavior, smoke can also affect resource quality. Tan et al. [71] found that caterpillars feeding on smoke-exposed plants had reduced development and weight. Furthermore, smoke from a Russian megafire was believed to have caused changes in plant phenology and ozone damage to plants [72]. The ash and smoke of megafires can be contaminated by burnt human infrastructure, which may have consequences for insect health. Months after the Notre-Dame fire in France, increased lead concentrations were found in honey from beehives downwind [73]. Overall, the severity and extent of megafire smoke impacts are unknown; however, Australian megafire smoke reached South America in a week and caused phytoplankton blooms across the South Pacific Ocean [74], revealing that significant impacts of megafires can be felt across vast distances.

Conservation

In ecosystems naturally prone to wildfires, historical regimes are essential disturbances that maintain ecological balance and are essential to insect communities. However, in these ecosystems where fire suppression practices have been in place for decades to over a century resulting in the buildup of fuels and altering the ecological trajectories of the insect communities. Prescribed burns that restore historic fire regimes can improve insect habitat [8,9] and control fuels, decreasing the likelihood of megafire development and spread. Although, some future megafires may be unavoidable.

However, we may be able to reduce their impacts. Where possible, land managers can create topographic controls such as fire roads, cutlines, and green breaks, to protect patches from burning and reduce burn severity. These tools can increase refugia aiding in insect survival during fire and ecosystem recovery. The use of fire controls has proven successful in insect conservation. During a Canadian megafire, cutlines burned at lower severity protecting butterflies from fire [75]. Furthermore, green breaks (planted lines of fire-retardant vegetation) have been shown to increase postfire biodiversity with lower maintenance costs than fire roads [76]. Green breaks also provide immediate habitat and food sources for insects postfire [37]. Creating anthropogenic fire refugia has great potential for reducing megafire damage, as even unburned patches as small as a square meter can be beneficial in ecosystem recovery [23].

Incorporating insects into conservation plans is crucial. Management plans should prioritize conserving at-risk species, such as those with restricted ranges, smaller body sizes, higher specialization, and lower abundances prefire [34]. Additionally, postfire efforts can aid insect recovery. Planting artificial bee nesting sites can increase bee populations and reduce the risk of extinction when minimal postfire habitat remains [77]. Fire management plans often focus on vertebrate species, neglecting invertebrates that are equally threatened and vital for ecosystem functioning through pollination, decomposition, and linking trophic interactions.

Last, post-megafire landscapes may present us opportunities to restore historical fire regimes and revitalize the health of long fire-suppressed ecosystems. Where areas have been fire-suppressed and vegetation has been overgrown, megafires may return the habitat to a more natural state, benefiting insects. After over 100 years of fire suppression in a boreal forest, a large wildfire resulted in increases in beetle assemblages postfire [78]. Megafires consume excessive fuels and overgrown vegetation, restoring historical fire regimes using prescribed burns may be more feasible. Implementing prescribed burn management will benefit insects and their habitats [9] and could reduce the risk of future megafires, minimizing further insect loss.

Conclusions

Megafires and extreme fire behaviors are becoming more prevalent [1,5,79], yet research on their impacts on insects and comparisons with historical regimes remain limited. Most existing megafire–insect studies originate from a single event, the Australian 2019–2020 bushfire season, despite the global occurrence of megafires. Existing research is further constrained by a lack of prefire data [16•,36••], including species descriptions, ranges,

and comprehensive inventories of insect communities. This absence of these data leads to significant underestimations of megafire effects on insects [16•] and limits insect conservation efforts [37]. As megafires become more common, we can expect losses of insect species, shifts in communities, and altering ecosystem functioning. These effects could potentially result in ecosystem collapses. To better understand and mitigate these effects, more research on insect responses to megafires is needed, along with efforts to identify vulnerable species and communities, as well as assessments of adaptive capacity in the face of changing fire regimes. Additionally, comprehensive insect community inventories of and species range descriptions are needed to identify how megafires affect species populations and ranges. These surveys could identify undescribed and undiscovered species that play important roles in ecosystems before they are lost. Finally, developing innovative solutions for insect conservation in the face of megafires is essential for preserving ecosystems.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

None.

Acknowledgements

We express our gratitude to the EECB Plant Insect Group for providing valuable feedback and inspiration during the development of this paper. This work was supported by the National Science Foundation [EF-2133818] and the United States Forest Service [22-DG-11132762-058].

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Duane A, Castellnou M, Brotons L: **Towards a comprehensive look at global drivers of novel extreme wildfire events.** *Clim Change* 2021, **165**, <https://doi.org/10.1007/s10584-021-03066-4>
 2. Le Breton TD, Lyons MB, Nolan RH, Penman T, Williamson GJ, Ooi MKJ: **Megafire-induced interval squeeze threatens vegetation at landscape scales.** *Front Ecol Environ* 2022, **20**:327–334.
 3. Collins L, Bradstock RA, Clarke H, Clarke MF, Nolan RH, Penman TD: **The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire.** *Environ Res Lett* 2021, **16**:e044029, <https://doi.org/10.1088/1748-9326/abeb9e>
 4. Linley GD, Jolly CJ, Doherty TS, Geary WL, Armenteras D, Belcher CM, Bliege Bird R, Duane A, Fletcher MS, Giorgis MA, et al.: **What do you mean, 'megafire'?** *Glob Ecol Biogeogr* 2022, **31**:1906–1922.
- The author discusses ambiguity in the use of the term 'megafire' and creates a clear definition. Megafires are defined as fire over 10 000 ha.
5. Nolan RH, Anderson LO, Poulter B, Varner JM: **Increasing threat of wildfires: the year 2020 in perspective: a global ecology and**

- biogeography special issue. *Glob Ecol Biogeogr* 2022, **31**:1898-1905.
6. Jones B, Kolden C, Jandt R, Abatzoglou J, Urban F, Arp C: **Fire behavior, weather, and burn severity of the 2007 anaktuvuk river tundra fire, North Slope, Alaska.** *Arct Antarct Alp Res* 2009, **41**:309-316.
 7. Harvey JA, Tougeron K, Gols R, Heinen R, Abarca M, Abram PK, Basset Y, Berg M, Boggs C, Brodeur J, et al.: **Scientists' warning on climate change and insects.** *Ecol Monogr* 2022, **93**:1553.
 8. Koltz AM, Burkle LA, Pressler Y, Dell JE, Vidal MC, Richards LA, Murphy SM: **Global change and the importance of fire for the ecology and evolution of insects.** *Curr Opin Insect Sci* 2018, **29**:110-116.
 9. Swengel AB: **A literature review of insect responses to fire, compared to other conservation managements of open habitat.** *Biodivers Conserv* 2001, **10**:1141-1169.
 10. Gutowski JM, Sućko K, Borowski J, Kubisz D, Mazur MA, Melke A, Mokrzycki T, Plewa R, Żmihorski M: **Post-fire beetle succession in a biodiversity hotspot: Białowieża Primeval Forest.** *Ecol Manag* 2020, **461**:117893.
 11. Bieber BV, Vyas DK, Koltz AM, Burkle LA, Bey KS, Guzinski C, Murphy SM, Vidal MC: **Increasing prevalence of severe fires change the structure of arthropod communities: evidence from a meta-analysis.** *Funct Ecol* 2022, **37**:2096-2109.
- This meta-analysis tested how fire management regimes, severity, and time since fire affect arthropod populations and communities. Arthropod communities vary in their responses to fire, but, generally, high fire severity decreases the metrics of diversity, while low severity increases them.
12. Mason SC, Shirey V, Ponisio LC, Gelhaus JK: **Response from bees, butterflies, and ground beetles to different fire and site characteristics: a global meta-analysis.** *Biol Conserv* 2021, **261**:109265.
 13. Liu Y, Wooster MJ, Grosvenor MJ, Lim KS, Francis RA: **Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.).** *Ecol Entomol* 2021, **46**:195-208.
 14. Liu Y, Francis RA, Wooster MJ, Grosvenor MJ, Yan S, Roberts G: **Systematic mapping and review of Landscape Fire Smoke (LFS) exposure impacts on insects.** *Environ Entomol* 2022, **51**:871-884.
- Lui et al. reviewed 42 studies on the effects of smoke on insects. Smoke can cause insect mortality as well as changes in behavior and development.
15. Rodriguez B, Lareau NP, Kingsmill DE, Clements CB: **Extreme pyroconvective updrafts during a megafire.** *Geophys Res Lett* 2020, **47**, <https://doi.org/10.1029/2020GL089001> e2020GL089001.
 16. Saunders ME, Barton PS, Bickerstaff JRM, Frost L, Latty T, Lessard BD, Lowe EC, Rodriguez J, White TE, Umbers KDL: **Limited understanding of bushfire impacts on Australian invertebrates.** *Insect Conserv Divers* 2021, **14**:285-293.
- This study documents the disparity in invertebrate research and conservation funding following the Australian 2019–2020 megafires.
17. Dell J, O'Brien J, Doan L, Richards L, Dyer L: **An arthropod survival strategy in a frequently burned forest.** *Ecology* 2017, **98**:2972-2974.
 18. Zaitsev AS, Gongalsky KB, Persson T, Bengtsson J: **Connectivity of litter islands remaining after a fire and unburnt forest determines the recovery of soil fauna.** *Appl Soil Ecol* 2014, **83**:101-108.
 19. Gandhi KJK, Spence JR, Langor DW, Morgantini LE: **Fire residuals as habitat reserves for epigeic beetles (Coleoptera: Carabidae and Staphylinidae).** *Biol Conserv* 2001, **102**:131-141.
 20. Bhaskar D, Easa PS, Sreejith KA, Skejo J, Hochkirch A: **Large scale burning for a threatened ungulate in a biodiversity hotspot is detrimental for grasshoppers (Orthoptera: Caelifera).** *Biodivers Conserv* 2019, **28**:3221-3237.
 21. Stevens JT, Collins BM, Miller JD, North MP, Stephens SL: **Changing spatial patterns of stand-replacing fire in California conifer forests.** *Ecol Manag* 2017, **406**:28-36.
 22. Gustafsson L, Berglind M, Granström A, Grelle A, Isacson G, Kjellander P, Larsson S, Lindh M, Pettersson LB, Strenghom J, et al.: **Rapid ecological response and intensified knowledge accumulation following a north European mega-fire.** *Scand J Res* 2019, **34**:234-253.
 23. Blomdahl EM, Kolden CA, Meddens AJH, Lutz JA: **The importance of small fire refugia in the central Sierra Nevada, California, USA.** *Ecol Manag* 2019, **432**:1041-1052.
 24. Mackey B, Lindenmayer D, Norman P, Taylor C, Gould S: **Are fire refugia less predictable due to climate change?** *Environ Res Lett* 2021, **16**:e114028, <https://doi.org/10.1088/1748-9326/ac2e88>
 25. Ruchin AB, Egorov LV, MacGowan I, Makarkin VN, Antropov AV, Gornostaev NG, Khapugin AA, Dvořák L, Esin MN: **Post-fire insect fauna explored by crown fermental traps in forests of the European Russia.** *Sci Rep* 2021, **11**, <https://doi.org/10.1038/s41598-021-00816-3>
 26. Dickman CR: **Ecological consequences of Australia's "Black Summer" bushfires: managing for recovery.** *Integr Environ Assess Manag* 2021, **17**:1162-1167.
 27. Wintle BA, Legge S, Woinarski JCZ: **After the megafires: what next for Australian wildlife?** *Trends Ecol Evol* 2020, **35**:753-757.
 28. Moir ML, Young DA: **Insects from the southwest Australia biodiversity hotspot: a barometer of diversity and threat status of nine host-dependent families across three orders.** *J Insect Conserv* 2022, **27**:3-18.
- This research evaluates the status of nine host-dependent insect families in three orders. In the status evaluations, host-insect coextinctions, climate change, altered fire regimes, habitat loss, and host population fragmentation threats were considered.
29. Moir ML: **Coextinction of *Pseudococcus markharveyi* (Hemiptera: Pseudococcidae): a case study in the modern insect extinction crisis.** *Aust Entomol* 2021, **60**:89-97.
 30. Dorey JB, Rebola CM, Davies OK, Prendergast KS, Parslow BA, Hogendoorn K, Leijts R, Hearn LR, Leitch EJ, O'Reilly RL, et al.: **Continental risk assessment for understudied taxa post-catastrophic wildfire indicates severe impacts on the Australian bee fauna.** *Glob Chang Biol* 2021, **27**:6551-6567.
 31. Braby MF: **Threatened species conservation of invertebrates in Australia: an overview.** *Aust Entomol* 2018, **57**:173-181.
 32. Cleary DFR, Genner MJ: **Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo.** *Glob Ecol Biogeogr* 2004, **13**:129-140.
 33. Hirowatari T, Makihara H: **Sugiarto: effects of fires on butterfly assemblages in lowland dipterocarp forest in East Kalimantan.** *Entomol Sci* 2007, **10**:113-127.
 34. Charrette NA, Cleary DFR, Moors A: **Range-restricted, specialist Bornean butterflies are less likely to recover from ENSO-induced disturbance.** *Ecology* 2006, **87**:2330-2337.
 35. Gonçalves TF, Correa CMA, Audino LD, Vaz-de-Mello FZ, Fontoura FM, Guedes NMR: **Quantifying the post-fire recovery of taxonomic and functional diversity of dung beetles in the Brazilian Pantanal.** *Ecol Entomol* 2022, **47**:601-612.
 36. Marsh JR, Bal P, Fraser H, Umbers K, Latty T, Greenville A, Rumpff L, Woinarski JCZ: **Accounting for the neglected: invertebrate species and the 2019–2020 Australian megafires.** *Glob Ecol Biogeogr* 2022, **31**:2120-2130.
- The authors measured the extent of the overlap of the 2019–2020 Australian megafires with ranges of invertebrate species. The megafires consumed over 50% of ~800 invertebrates' ranges.
37. Sands DPA: **Important issues facing insect conservation in Australia: now and into the future.** *Aust Entomol* 2018, **57**:150-172.
 38. Rangel-Acosta JL, Martínez-Hernández NJ, Yonoff-Zapata R: **Response of dung beetles (Scarabaeidae: Scarabaeinae) to habitat modification caused by a forest fire in the Bijibana Reserve, Atlántico-Colombia.** *Rev Mex Biodivers* 2020, **91**:e912879, <https://doi.org/10.22201/ib.20078706e.2020.91.2879>

39. Mutz J, Underwood N, Inouye BD: **Time since disturbance affects colonization dynamics in a metapopulation.** *J Anim Ecol* 2017, **86**:1065-1073.
 40. Brennan KEC, Moir ML, Wittkuhn RS: **Fire refugia: the mechanism governing animal survivorship within a highly flammable plant.** *Austral Ecol* 2011, **36**:131-141.
 41. Driscoll DA, Armenteras D, Bennett AF, Brotons L, Clarke MF, Doherty TS, Haslem A, Kelly LT, Sato CF, Sitters H, et al.: **How fire interacts with habitat loss and fragmentation.** *Biol Rev* 2021, **96**:976-998.
 42. Knight TM, Holt RD: **Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem.** *Ecology* 2005, **86**:587-593.
 43. Arnold KT, Murphy NP, Gibb H: **Post-fire recovery of litter detritivores is limited by distance from burn edge.** *Austral Ecol* 2017, **42**:94-102.
 44. Nimmo DG, Avitabile S, Banks SC, Bliege Bird R, Callister K, Clarke MF, Dickman CR, Doherty TS, Driscoll DA, Greenville AC, et al.: **Animal movements in fire-prone landscapes.** *Biol Rev* 2019, **94**:981-998.
 45. Favarin S, Fantinato E, Buffa G: **Pollinator distribution in patches of suitable habitat depends more on patch isolation than on floral abundance.** *Flora* 2022, **296**, <https://doi.org/10.1016/j.flora.2022.152165>
 46. Collinge SK, Palmer TM: **The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands.** *Land Ecol* 2002, **17**:647-656.
 47. Grez AA, Prado E: **Effect of plant patch shape and surrounding vegetation on the dynamics of predatory Coccinellids and their prey *Brevicoryne brassicae* (Hemiptera: Aphididae).** *Environ Entomol* 2000, **29**:1244-1250.
 48. Marschalek DA, Deutschman DH, Strahm S, Berres ME: **Dynamic landscapes shape post-wildfire recolonisation and genetic structure of the endangered Hermes copper (*Lycaena hermes*) butterfly.** *Ecol Entomol* 2016, **41**:327-337.
 49. Dell JE, Salcido DM, Lumpkin W, Richards LA, Pokswinski SM, Loudermilk EL, O'Brien JJ, Dyer LA: **Interaction diversity maintains resiliency in a frequently disturbed ecosystem.** *Front Ecol Evol* 2019, **7**, <https://doi.org/10.3389/fevo.2019.00145>
 50. Banza P, Macgregor CJ, Belo ADF, Fox R, Pocock MJO, Evans DM: **Wildfire alters the structure and seasonal dynamics of nocturnal pollen-transport networks.** *Funct Ecol* 2019, **33**:1882-1892.
 51. McLaughlin JP, Schroeder JW, White AM, Culhane K, Miris HE, Tarbill GL, Sire L, Page M, Baker EJ, Moritz M, et al.: **Food webs for three burn severities after wildfire in the Eldorado National Forest, California.** *Sci Data* 2022, **9**, <https://doi.org/10.1038/s41597-022-01220-w>
 52. Thom MD, Daniels JC, Kobziar LN, Colburn JR: **Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida.** *PLoS One* 2015, **10**:e0126755, <https://doi.org/10.1371/journal.pone.0126755>
 53. Johnson SD, Horn KC, Savage AM, Windhager S, Simmons MT, Rudgers JA: **Timing of prescribed burns affect abundance and composition of arthropods in the Texas hill country.** *Southwest Nat* 2008, **53**:137-145.
 54. Decker BL, Harmon-Threatt AN: **Growing or dormant season burns: the effects of burn season on bee and plant communities.** *Biodivers Conserv* 2019, **28**:3621-3631.
 55. Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MKJ, Ruthrof KX, Miller BP: **Mechanisms of fire seasonality effects on plant populations.** *Trends Ecol Evol* 2019, **34**:1104-1117.
 56. Robertson B, Rebar D: **Timing of prescribed burns impacts plant diversity but not investment in pollinator recruitment in a tallgrass prairie.** *Ecosphere* 2022, **13**:e3914, <https://doi.org/10.1002/ecs2.3914>
 57. Bergstrom DM, Wienecke BC, van den Hoff J, Hughes L, Lindenmayer DB, Ainsworth TD, Baker CM, Bland L, Bowman DMJS, Brooks ST, et al.: **Combating ecosystem collapse from the tropics to the Antarctic.** *Glob Chang Biol* 2021, **27**:1692-1703.
 58. Gallagher RV, Allen S, Mackenzie BDE, Yates CJ, Gosper CR, Keith DA, Merow C, White MD, Wenk E, Maitner BS, et al.: **High fire frequency and the impact of the 2019-2020 megafires on Australian plant diversity.** *Divers Distrib* 2021, **27**:1166-1179.
 59. Garcia LC, Szabo JK, de Oliveira Roque F, de Matos Martins Pereira A, Nunes da Cunha C, Damasceno-Júnior GA, Morato RG, Tomas WM, Libonati R, Ribeiro DB: **Record-breaking wildfires in the world's largest continuous tropical wetland: integrative fire management is urgently needed for both biodiversity and humans.** *J Environ Manag* 2021, **293**:e112870, <https://doi.org/10.1016/j.jenvman.2021.112870>
 60. Nimmo DG, Carthey AJR, Jolly CJ, Blumstein DT: **Welcome to the Pyrocene: animal survival in the age of megafire.** *Glob Chang Biol* 2021, **27**:5684-5693.
 61. Gerson EA, Kelsey RG: **Attraction and direct mortality of pandora moths, *Coloradia pandora* (Lepidoptera: Saturniidae), by nocturnal fire.** *Ecol Manag* 1997, **98**:71-75.
 62. De Alcantara Viana JV, Lourenço Garcia de Brito V, de Melo C: **Colour matching by arthropods in burned and unburned backgrounds in a Neotropical savanna.** *Austral Ecol* 2022, **47**:1427-1437.
 63. Kay CB, Delehanty DJ, Pradhan DS, Grinath JB: **Climate change and wildfire-induced alteration of fight-or-flight behavior.** *Clim Chang Ecol* 2021, **1**:e112870, <https://doi.org/10.1016/j.ecochg.2021.100012>.
- Wildfire can affect stress responses of the thatch ant (*Formica obscuripes*). In recently burned environments, ants are more likely to flee than attack threatening stimuli to defend their colonies.
64. Watts CH, Didham RK: **Rapid recovery of an insect-plant interaction following habitat loss and experimental wetland restoration.** *Oecologia* 2006, **148**:61-69.
 65. Henry SC, Kirkpatrick JB, McQuillan PB: **The half century impact of fire on invertebrates in fire-sensitive vegetation.** *Austral Ecol* 2022, **47**:590-602.
 66. Talucci AC, Loranty MM, Alexander HD: **Siberian taiga and tundra fire regimes from 2001-2020.** *Environ Res Lett* 2022, **17**:e025001, <https://doi.org/10.1088/1748-9326/ac3f07>
 67. Heim RJ, Heim W, Bültmann H, Kamp J, Rieker D, Yurtaev A, Hölzel N: **Fire disturbance promotes biodiversity of plants, lichens and birds in the Siberian subarctic tundra.** *Glob Chang Biol* 2022, **28**:1048-1062.
 68. Brower LP, Malcolm SB: **Animal migrations: endangered phenomena.** *Am Zool* 1991, **31**:265-276.
 69. Brower LP, Calvert WH, Hedrick LE, Christian J: **Biological observations on an overwintering colony of Monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico.** *J Lepid Soc* 1977, **31**:232-242.
 70. Hegedüs R, Åkesson S, Horváth G: **Anomalous celestial polarization caused by forest fire smoke: why do some insects become visually disoriented under smoky skies?** *Appl Opt* 2007, **46**:2717-2726.
 71. Tan YQ, Dion E, Monteiro A: **Haze smoke impacts survival and development of butterflies.** *Sci Rep* 2018, **8**:e15667, <https://doi.org/10.1038/s41598-018-34043-0>
 72. Wang J, Zhang X: **Investigation of wildfire impacts on land surface phenology from MODIS time series in the western US forests.** *P&RS* 2020, **159**:281-295.
 73. Smith KE, Weis D, Chauvel C, Moulin S: **Honey maps the Pb fallout from the 2019 fire at Notre-Dame Cathedral, Paris: a geochemical perspective.** *Environ Sci Technol Lett* 2020, **7**:753-759.
 74. Wang Y, Chen HH, Tang R, He D, Lee Z, Xue H, Wells M, Boss E, Chai F: **Australian fire nourishes ocean phytoplankton bloom.** *Sci Total Environ* 2022, **807**:150775, <https://doi.org/10.1016/j.scitotenv.2021.150775>

75. Riva F, Pinzon J, Acorn JH, Nielsen SE: **Composite effects of cutlines and wildfire result in fire refuges for plants and butterflies in boreal treed peatlands.** *Ecosystems* 2020, **23**:485-497.
76. Cui X, Alam MA, Perry GL, Paterson AM, Wyse SV, Curran TJ: **Green firebreaks as a management tool for wildfires: lessons from China.** *J Environ Manag* 2019, **233**:329-336.
77. Hogendoorn K, Glatz RV, Leijds R: **Conservation management of the green carpenter bee *Xylocopa aerata* (Hymenoptera: Apidae) through provision of artificial nesting substrate.** *Aust Entomol* 2021, **60**:82-88.
78. Johansson T, Andersson J, Hjältén J, Dynesius M, Ecker F: **Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression.** *Insect Conserv Divers* 2011, **4**:142-151.
79. Varga K, Jones C, Trugman A, Carvalho LMV, McLoughlin N, Seto D, Thompson C, Daum K: **Megafires in a warming world: what wildfire risk factors led to California's largest recorded wildfire.** *Fire* 2022, **5**, <https://doi.org/10.3390/fire5010016>