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3 Main Manuscript for

4 Impacts of fire and prospects for recovery in a tropical peat forest 5 ecosystem

6

7 Mark E. Harrison^{a,b,c,1,2}, Nicolas J. Deere^{d,1,2}, Muhammad Ali Imron^e, Darmae Nasir^f, Adul, Hastin

8 Ambar Asti^e, Joana Aragay Soler^g, Nicholas C. Boyd^h, Susan M. Cheyneⁱ, Sarah A. Collins^j, Laura J.

9 D'Arcy^k, Wendy M. Erb^l, Hannah Greenⁱ, William Healy^a, Hendri^m, Brendan Hollyⁿ, Peter R. Houlihan^o,

10 Simon J. Husson^k, Iwan^m, Karen A. Jeffersⁱ, Ici P. Kulu^f, Kitso Kusin^f, Nicholas C. Marchant^g, Helen C.

11 Morrogh-Bernard^{a,c}, Susan E. Page^b, Ari Purwanto^m, Bernat Ripoll Capilla^k, Oscar Rodriguez de

12 Rivera Ortega^p, Santiano^m, Katie L. Spencer^d, Jito Sugardjito^{q,r}, Jatna Supriatna^s, Sara A. Thornton^{b,t},

13 F. J. Frank van Veen^{a,c}, Yulintine^f, Matthew J. Struebig^d

14

15 ^{a.} Centre for Ecology and Conservation, Faculty of Environment, Science and Economy,
16 University of Exeter, Penryn, TR10 9FE, United Kingdom.

17 ^{b.} School of Geography, Geology and the Environment, University of Leicester, Leicester, LE1
18 7RH, UK

19 ^{c.} Current address: Department of Geography, Faculty of Environment, Science and Economy,
20 University of Exeter, Penryn, TR10 9FE, UK

21 ^{d.} Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and
22 Conservation, University of Kent, Canterbury, CT2 7NR, UK

23 ^{e.} Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta 55281, Indonesia

24 ^{f.} Centre for the International Cooperation in Sustainable Management of Tropical Peatlands,
25 University of Palangka Raya, Palangka Raya 73112, Indonesia

26 ^{g.} Wildlife Conservation Research Unit, Department of Biology, University of Oxford, Oxford,
27 OX13 5QL, UK

28 ^{h.} University of Wales Aberystwyth, Aberystwth, SY23 1DE, UK

29 ^{i.} School of Humanities and Social Sciences, Oxford Brookes University, Oxford, OX3 0BP, UK

- 30 j. School of Biological and Marine Sciences, Faculty of Science and Engineering, University of
31 Plymouth, Plymouth, PL4 8AA, UK
- 32 k. Borneo Nature Foundation International, Tremough Innovation Centre, Penryn, TR10 9TA,
33 UK
- 34 l. K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell
35 University, Ithaca, New York 14850, USA
- 36 m. Yayasan Borneo Nature Indonesia, Jl. Bukit Raya No. 17, Palangka Raya 73112, Central
37 Kalimantan, Indonesia
- 38 n. Environmental Studies, Centre College, Danville, KY 40422, USA
- 39 o. UCLA Center for Tropical Research, Institute of the Environment and Sustainability, Los
40 Angeles, CA 90095-1496, USA
- 41 p. Department of Mathematics and Statistics, Faculty of Environment, Science and Economy,
42 University of Exeter, Streatham Campus, Exeter, EX4 4QF, UK.
- 43 q. Centre for Sustainable Energy and Resources Management, Universitas Nasional, Jakarta
44 12520, Indonesia
- 45 r. Faculty of Biology, Universitas Nasional, Jakarta 12520, Indonesia
- 46 s. Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Indonesia,
47 Depok 16424, Indonesia
- 48 t. Current address: Wildfowl and Wetlands Trust, Slimbridge, Gloucester, GL2 7BT, UK

49 ¹ M.E.H. and N.J.D. contributed equally to this work.

50 ² To whom correspondence may be addressed. Email: M.E.Harrison@exeter.ac.uk (M.E.H.);
51 N.J.Deere@kent.ac.uk (N.J.D)

52

53 **Author Contributions:** conceived the idea: M.E.H., N.J.D., M.A.I., D.N., S.M.C., S.J.H., H.C.M.-B.,
54 S.E.P., B.R.C., F.J.F.v.V., M.J.S.; Performed research and contributed data: M.E.H., M.A.I., D.N., A.,
55 H.A.A., J.A.S., N.C.B., S.M.C., L.J.D., W.M.E., W.H., H., B.H., P.R.H., S.J.H., I., K.A.J., I.P.K., K.K.,
56 N.C.M., H.C.M.-B., A.P., B.R.C., J.Sug., J.Sup., S., S.A.T., Y.; Processed data M.E.H., N.J.D.,
57 S.M.C., S.A.C., H.G., K.L.S.; Analyzed data: N.J.D. with support from O.R.d.R.O.; Wrote the paper:
58 M.E.H., N.J.D., M.J.S., with support and feedback from all authors. Both M.E.H and N.J.D contributed
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63

64 **This PDF includes:**

65 **Main text**

66 **Figures 1 to 4**

67 **Abstract**

68

69 Uncontrolled fires place considerable burdens on forest ecosystems, compromising our ability to meet
70 conservation and restoration goals. A poor understanding of the impacts of fire on ecosystems and
71 their biodiversity exacerbates this challenge, particularly in tropical regions where few studies have
72 applied consistent analytical techniques to examine a broad range of ecological impacts over multi-
73 year timeframes. We compiled 16 years of data on ecosystem properties (17 variables) and
74 biodiversity (21 variables) from a tropical peatland in Indonesia to assess fire impacts and infer the
75 potential for recovery. Burned forest experienced altered structural and microclimatic conditions,
76 resulting in a proliferation of non-forest vegetation and erosion of forest ecosystem properties and
77 biodiversity. Compared to unburned forest, habitat structure, tree density, and canopy cover
78 deteriorated by 58-98%, while declines in species and populations were most pronounced for trees,
79 damselflies, and butterflies, particularly for forest specialist species. Tracking ecosystem property and
80 biodiversity datasets over time revealed most to be sensitive to recurrent high-intensity fires within the
81 wider landscape. These megafires immediately compromised water quality and tree reproductive
82 phenology, crashing commercially valuable fish populations within 3 months and driving a gradual
83 decline in threatened vertebrates over 9 months. Burned forest remained structurally compromised
84 long after a burn event, but vegetation showed some signs of recovery over a 12-year period. Our
85 findings demonstrate that, if left uncontrolled, fire may be a pervasive threat to the ecological
86 functioning of tropical forests, underscoring the importance of fire prevention and long-term
87 restoration efforts, as exemplified in Indonesia.

88

89 **Significance Statement**

90

91 Fire management in tropical forests requires an understanding of the ecological impacts of burn
92 events and the ecosystem's capacity to recover. We investigate this by tracking multiple ecosystem
93 properties and biodiversity variables over 16 years in a tropical peatland in Indonesia. Compared to
94 unburned areas, burned forest contained fewer trees, was more open and hotter, and contained more
95 non-forest vegetation, leading to reduced biodiversity. Tracking ecological variables in non-burned
96 forest over time revealed the ecosystem's sensitivity to recurrent, high-intensity fire within the wider

97 landscape. Some recovery was evident in burned areas within 12 years, but repeated fire risks
98 reversing this trend. While fire prevention is crucial, long-term, context-specific tropical forest
99 restoration is needed to deal with the consequences of fire.

100

101 **Main Text**

102

103 **Introduction**

104

105 Fire is a powerful biological filter, influencing the successional dynamics of terrestrial ecosystems and
106 the distribution of wildlife (1, 2). However, environmental change driven by anthropogenic activities
107 disrupts natural fire regimes across the world, increasing the prevalence and impacts of fire (3). In
108 particular, large-scale “megafires” are a global phenomenon causing major ecological disruption (4).
109 Fire accounts for 41% of tropical forest loss globally (5) and at least 1,071 species across nine
110 taxonomic groups are reported as threatened by altered fire regimes (6). Most of our understanding of
111 the ecological impacts of fire comes from naturally fire-prone habitats (e.g., savannahs), with limited
112 information available from humid tropical regions, which tend to comprise fire-sensitive ecosystems
113 (7, 8). With global fire activity and impacts projected to increase alongside changes in climate and
114 land use (3, 9), detailed insights into ecosystem-scale responses to fire are urgently needed to help
115 safeguard the ecological integrity of fire-affected tropical biomes and prevent species extinctions.

116 The impacts of burning are most pronounced in ecosystems where fire is naturally rare (10).
117 Tropical forests are particularly maladapted to tolerate and recover from fire-related damage, which
118 impacts ecosystem functioning, regeneration dynamics and carbon emissions (11, 12). Fire-induced
119 tree mortality causes a marked change in forest structure (13, 14), facilitating compositional
120 transitions that favor herbaceous vegetation and disturbance-tolerant pioneer species (15, 16). Such
121 structural and compositional shifts can alter microclimatic conditions and increase the prevalence of
122 flammable vegetation, leaving the ecosystem susceptible to recurrent fire (11). Fires can also cause
123 extensive wildlife mortality and other health and behavioral impacts, due to immolation, radiant heat
124 and toxic particulate inhalation (17-19). Subsequent deterioration or loss of vertebrate-mediated
125 ecological processes may then influence post-fire vegetation recovery (20), amplifying a feedback
126 loop that compromises the future of the forest ecosystem. While current evidence indicates that

127 ecological responses to fire are intricately linked, it is challenging to draw parallels amongst multiple
128 studies while accounting for confounding effects of study design, geographic location and disturbance
129 legacies. Ecosystem-scale syntheses that better control for these confounding effects are necessary if
130 we are to reliably compare fire impacts across multiple ecological components and infer interactions
131 between fire, vegetation dynamics and biodiversity.

132 The characteristics of the fire regime govern the recovery potential of burned ecosystems
133 (21). Fire intensity underpins the magnitude of ecological damage, while fire frequency, within and
134 between fire seasons, determines fire recurrence in a given area. Collectively, these characteristics
135 dictate an ecosystem's capacity to resist change and return to its pre-disturbance state (21).
136 Recurrent, high-intensity fires thus threaten ecosystem stability and increase the risk of irreversible
137 state shifts (22), with potentially grave consequences for biodiversity (6, 20). While proximity to a fire
138 determines much of its impact, indirect consequences of fire, primarily via smoke or haze exposure,
139 can extend the footprint of disturbance far beyond the burn extent (23).

140 The essential longitudinal data needed to track ecological trends relative to fire regimes are
141 so far missing from appraisals of fire in tropical ecosystems. To date, most ecological assessments
142 have compared properties of burned and unburned areas, but have not examined both spatial and
143 temporal variability in fire regimes (24). Such insights are particularly lacking for tropical peatlands,
144 such as those in Indonesia, which are highly valued for their globally significant carbon stocks and
145 biodiversity, but have become increasingly susceptible to fire in recent decades due to changing
146 climatic conditions and land-use practices (25). While the impacts of tropical peatland fires on carbon
147 emissions, public health, local communities and the economy are well documented (26, 27), their
148 ecological impacts remain relatively understudied, as does the ability of the ecosystem to regenerate
149 naturally following fire (though see, e.g., (28)).

150 Here, we conduct a comprehensive assessment of fire impacts on the structure, composition,
151 functioning and biodiversity of a forested tropical ecosystem. We have focused on a 16-year dataset
152 from a 320-km² tropical peat-swamp forest research area in Indonesian Borneo (Fig. 1). The area is
153 particularly important to study because of its fire history, comprising burned areas in various stages of
154 recovery interspersed within unburned forest subject to indirect impacts of fire within the wider
155 landscape. Tropical peatland fires are exacerbated by peatland drainage and are typically
156 anthropogenic in origin, in this region being predominantly driven by slash-and-burn agricultural

157 practices, plus use of fire to clear areas for fishing and in land tenure conflicts (29-31). Peatland fires
158 may smolder for days or even months, until extinguished by human intervention or rain.

159 Drawing on a matched analytical framework, we examine the ecological impacts of burn
160 events, and extend this to explore the fire regime characteristics driving ecological disruption and the
161 potential for natural recovery in fire-sensitive forest ecosystems. We synthesized 27 ecological
162 component datasets to explore how fire affects core ecosystem properties (i.e., the abiotic, structural
163 and functional alterations directly attributed to fire exposure) and biodiversity (i.e., an emergent
164 feature of both fire and the alteration of the ecosystem properties, partitioned into forest specialist and
165 all species) (Table S1a). We systematically compared areas subjected to a recent severe burn event
166 (*new burn*; burned 1.5-5 years prior to surveys), with those recovering from historical fires (*old burn*,
167 burned 10-21 years prior) and an adjacent relatively undisturbed peat-swamp forest (*unburned*).

168 To examine the sensitivity of ecosystem dynamics within forest areas to temporal variations in
169 fire within the wider landscape (fire frequency and intensity based on satellite data), we collated
170 longitudinal data on a further nine ecological components, comprising 236 sampling locations
171 spanning a 16-year period, thus allowing for detection of both immediate and graduated responses to
172 indirect fire impacts (Table S1b). Of particular interest was the impact of large-scale megafires, which
173 we quantified using a combination of spatial (distance to most recent megafire) and temporal (time
174 since last megafire) measures to understand the extent to which the indirect impacts emerging from
175 megafires permeate into adjacent habitat. The forest sampling locations incorporated in this part of
176 the study were positioned between 0.5 and 8.75 km from burned areas within the wider landscape
177 (Fig. 1). Using dynamic statistical frameworks, modified to account for imperfect detection where
178 appropriate, we reveal how tropical peat-swamp forests are affected by the spatial and temporal
179 footprint of fire.

180 This integrated spatiotemporal analytical framework enables us to test the hypotheses that
181 fire impacts in forested tropical ecosystems: (1) cause deterioration to ecological components in burn-
182 affected areas; (2) are mediated by fire regime characteristics, which indirectly extend the spatial
183 footprint of fire into adjacent unburned habitat; and (3) demonstrate some evidence of recovery
184 following longer post-fire intervals. Our results provide detailed insights into the impacts of fire in
185 tropical ecosystems and their potential for recovery, while demonstrating the importance of enhancing
186 fire management efforts in an increasingly flammable world.

187

188 **Results**

189

190 *Direct impacts of fire on the peatland ecosystem and potential for recovery*

191 Burned forest (both new and old burn treatments) was characterized by diminished ecosystem
192 properties and biodiversity compared to unburned controls (Fig. S1; see also Figs. S2-3 for modelled
193 mean values for all variables). We observed altered microclimatic conditions, a proliferation of non-
194 forest vegetation and an erosion of forest attributes and biodiversity, which disproportionately affected
195 forest-specialist taxa. Comparable effect sizes between aggregate ecosystem property and
196 biodiversity variables implied that impacts were consistent across both abiotic and biotic components
197 of the forest (Fig. S1). Moreover, at the aggregate level, there remained a high degree of overlap
198 between new and old burn treatments in the effect sizes for changes in ecosystem properties and
199 biodiversity (both all species and forest specialists), implying little evidence of post-fire recovery (Fig.
200 S1).

201 Coarse-scale aggregate trends masked considerable variation in the extent of fire impacts
202 within and between ecological datasets. For ecosystem properties, the strongest effects of burning
203 were evident for forest structure, tree density (across all stages of the life cycle) and canopy cover,
204 which declined by 58-98% when compared to unburned forest (Fig. 2). However, these impacts
205 tended to be more severe in newly burned areas, indicating some post-fire recovery over the 9-year
206 interval between burn treatments. Further evidence of compositional recovery was observed, with
207 higher densities of both seedlings and saplings in old compared to new burn areas. Similarly, the
208 rapid proliferation of invasive ferns observed in newly burned areas (> 1,000% increase in cover
209 compared to controls) was greatly reduced in old burn areas (Fig. 2). In contrast, daily maximum
210 temperature was higher in both burn treatments compared to unburned controls (old burn: 24%
211 increase; new burn: 21% increase), likely reflecting the substantial reductions in canopy cover (>
212 90%) consistent across both burn treatments (Fig. 2).

213 Burned areas generally contained fewer species, occurring at lower abundances; a finding
214 broadly consistent among biodiversity datasets. Impacts were most pronounced for non-pioneer tree
215 species, which were completely lost from all new burn areas, and forest specialist invertebrates,
216 which experienced declines of up to 99.9% in species richness and equivalent reductions in

217 abundance (Fig. 2). To a lesser extent, herpetofauna communities also contained fewer species (38-
218 65%) and exhibited population declines of between 43 and 90% in fire-affected areas, with reptiles
219 demonstrating a greater sensitivity to burn events. Forest soundscapes indicated variable responses
220 to fire among the acoustic indices quantified, but declines in the prevalence and intricacy of some
221 biotic signals in burn treatments were notable (up to 25% reduction; Fig. 2). Evidence of post-fire
222 recovery was more limited for biodiversity, but when comparisons between the old and new burn
223 treatments were available, tree species richness remained suppressed. In contrast, Odonata species
224 diversity rebounded (including 50 and 98% recovery of forest-specialist damselfly and dragonfly
225 species, respectively), albeit at reduced abundances, while avian soundscapes regained a degree of
226 acoustic complexity (Fig. 2).

227

228 *Indirect impacts: Temporal variation in peatland ecosystem dynamics relative to megafire events*

229 On average, 594 (range: 5 – 2,565) high-confidence fire detections were captured by MODIS satellites
230 annually across the study site and a 25 km buffer surrounding it (total area: 625 km²). For Central
231 Kalimantan province, this was extended to 11,779 (range: 528 – 38,002) detections. The ecological
232 time-series datasets from forest areas were sensitive to the six “megafire” events occurring between
233 2004 and 2020 within this wider study landscape (all species: Fig. 3; forest specialists: Fig. S4). We
234 define “megafires” based on statistically anomalous peaks in fire regime characteristics, identified as
235 months when both the frequency and summed radiative power of fire detections exceeded the 95th
236 percentile of the historical fire profile (Appendix S1). Comparing the average change in forest datasets
237 pre- and post-megafire revealed that impacts on ecosystem properties were greatest at the one-
238 month interval, where river pH became more acidic (posterior mean: -11.2%; 95% BCI: -12.7 to -
239 9.7%), and flower production (-21.3%, -59.5 to -2.8%) and leaf flush (-15.7%, -24.8 to -5.5%)
240 declined, coinciding with an increase in leaf-fall (26.7%, 8.2 to 61.9%).

241 For biodiversity, we built temporal profiles of occurrence data, defined as the probability that a
242 taxon, ecologically meaningful group (feeding guilds, threatened taxa, commercially valuable taxa) or
243 species was present within the study area against the backdrop of historical megafire events. At the
244 one-month interval, fish populations exhibited sharp decreases in occurrence (-67.9%, -84.5 to -
245 39.7%), with noteworthy reductions in forest specialists (-73.5%, -83.0 to -59.4%) and commercially-
246 valuable species (-29.2%, -60.9 to -0.3%). A decline in butterflies during the same timeframe was less

247 severe (-14.0%, -35.8 to -0.02%), with forest specialist species generally more robust to megafires in
248 the wider landscape (-5.7%, -27.3 to -21.8%). Mammals and ground-dwelling birds did not respond to
249 fire events within the wider landscape over time across all species together, but were sensitive across
250 longer timescales when analyses were based on threatened vertebrates (-19.8%, -40.3 to -0.07%,
251 six-month interval) and forest specialist birds (-46.2%, -70.9 to -0.01%; 12-month interval).

252 When analyses were restricted to the most severe megafire event in the time-series (2009;
253 Fig. 3), the above differences were exacerbated for most groups. Within one month following the 2009
254 megafires, flower and leaf production reduced by 45.4% (-52.8 to -37.6%) and 39.5% (-43.2 to -
255 35.9%), respectively, while, across longer timescales, fruits became less prevalent (-21.4%, -32.9 to -
256 6.6%; 9-month interval). Declines of threatened vertebrate species escalated (-29.5%, -49.6 to -3.2%;
257 9 month-interval), underpinned in part by a gradual erosion in mammal occurrence (-23.7%, -48.4 to -
258 0.01%; 12-month interval for all species, with no decline observed for forest specialists). However,
259 general taxonomic trends often obscured idiosyncratic responses at the guild and species levels
260 (Figs. S6-10). For example, over 12-months following the 2009 megafires, Sunda clouded leopard
261 (*Neofelis nebulos*) populations declined dramatically (-47.8%, -67.2 to -19.4%; Fig. S10), while
262 herbivorous mammal occurrence increased by 69.5% (15.8-123.2%; Fig. S6), demonstrating that
263 some species have capacity to capitalize on the ecological opportunities presented by fires.

264 The sensitivity of forest ecological components to megafires within the wider landscape was
265 driven by various, and often multiple, aspects of fire regimes, as illustrated in Fig. 4. For ecosystem
266 properties, patterns of river pH, leaf-fall and fruit production were most influenced by fire intensity (Fig.
267 4a). Fires characterized by a high radiative power resulted in acidic rivers, reduced leaf-fall and
268 greater fruit production. We also found moderate support for an influence of fire frequency on
269 ecosystem properties (Fig. 4a), with rivers becoming less acidic, fruit production increasing, leaf flush
270 decreasing and leaf-fall increasing with increasing time since fire. When we extended the analysis to
271 include the distances of our forest survey areas from fires (see Appendix S4.3.5), we discovered that
272 flowers and leaf flush tended to be abundant when fires were more distant (Fig. 4a).d With respect to
273 time, fruit and leaf flush production diminished and rivers became more acidic as more time had
274 elapsed since the last megafire event (Fig. 4a).

275 Biodiversity was highly sensitive to fire properties within the broader landscape, reflected in
276 the occupancy responses of fish, ground-dwelling birds and medium-large mammals (Fig 4b). These

277 taxa exhibited consistent non-linear associations with fire frequency, indicating a degree of fire
278 tolerance up to an inflection point, beyond which occupancy began to decline as fire frequency
279 increased. Inspection of the inflection points relative to fire frequency indicates that more mobile
280 species (e.g., mammals) tended to have a greater tolerance to fire than more sedentary taxa (e.g.
281 ground-dwelling birds, Fig. 4b). Fish and birds were also sensitive to fire radiative power, becoming
282 less prevalent with increasing fire intensity in the landscape. Butterfly occurrence was best modelled
283 by spatiotemporal proximity measures (Fig. 4b), demonstrating higher occupancy with increasing time
284 since megafires. An association of fish occupancy with time elapsed since the last megafire implies
285 that fish populations were heavily impacted by megafires initially, but began to rebound around four-
286 months after the event (Fig. 4b). Species-specific associations underpinning these coarse taxonomic
287 responses are presented in Figs. S8-11). When only forest specialist species were considered, we
288 found broadly consistent responses to fire incidence and properties across all taxonomic groups
289 (Figs. S4-5).

290

291 **Discussion**

292

293 Ecosystem-scale syntheses of tropical forests have been rarely featured in fire impact assessments,
294 despite these habitats being poorly adapted to, and heavily impacted by, fire (7, 8). We have
295 compared recently burned, old burned, and unburned areas in a 320 km² study area, and in so doing
296 reveal the pervasive impacts of fire in tropical forest, involving the progressive deterioration of both
297 ecosystem properties and biodiversity with important implications for recovery. For forest habitat in
298 the vicinity of burned areas, we show that indirect ecological disruption is driven by both the frequency
299 and intensity of the fire regime in the wider landscape, which often act together to erode the forest's
300 biological value and recovery potential.

301

302 *Ecological impacts of fire*

303 Our data indicate that the peat-swamp ecosystem experienced a cascading response to fire, with
304 burned areas characterized by the loss of large standing trees, triggering a sequence of structural,
305 microclimatic and compositional alterations. Tropical trees generally lack specialized traits to
306 withstand fire damage (32), resulting in substantial mortality (13), as evidenced by the complete loss

307 of forest specialist species from new burn areas in our study. Tree loss leads to architectural
308 simplification in tropical forests, increasing light availability, and creating hotter, drier microclimatic
309 conditions, favoring non-forest vegetation and pioneer species (11, 28). This includes invasive ferns,
310 which rapidly colonize and dominate the post-fire vegetation community in tropical peatlands,
311 hindering native tree seedling establishment (15). High community turnover and disruption to plant
312 demographic processes can result in long-term reductions in net primary productivity, nutrient cycling
313 and carbon storage in fire-affected forest areas (9, 33, 34). Similar post-fire trajectories have been
314 documented in Amazonia (e.g., (14, 16)), indicating that this may be a generalized response in fire-
315 sensitive forest formations.

316 Our results emphasize the sensitivity of tropical wildlife to fire, although the extent and
317 magnitude of fire impacts varied across taxa and were difficult to generalize, in common with other
318 assessments (8, 24). Across all taxonomic groups we assessed, forest specialists were found to be
319 highly sensitive to the direct impacts of fire, suggesting that burned areas undergo compositional
320 shifts in wildlife communities favouring disturbance-tolerant generalists. Such biotic homogenization is
321 well documented in degraded habitats and has the capacity to exacerbate disturbance impacts if the
322 remaining generalist species cannot provide compensatory ecological functions (35). The most
323 pronounced impacts in our study were on aquatic fauna (fish), as rivers became more acidic from the
324 leaching of dissolved organic carbon through burning (36). Fire impacts can be especially acute in
325 freshwater systems as disruption to water quality and sediment flux propagates downstream (e.g.,
326 Australia: (37), which may have particularly important impacts on local communities in tropical
327 peatlands, given their often high reliance on fishing (38).

328 Wildlife responses to fire emerge from a suite of direct and indirect drivers that can act in
329 isolation or synergistically. Fire can cause substantial direct mortality for tropical taxa (e.g., Brazil:
330 (17)), many of which do not possess the response strategies to detect and escape from incipient burn
331 events (18, 39). Fire can also affect wildlife indirectly through the disruption of forest phenological
332 events and microhabitat conditions, compromising habitat quality, microclimatic suitability and
333 resource provisioning, which have been documented to have insidious effects on animal populations
334 in the Amazon (40, 41). Moreover, exposure to toxic haze may be a pervasive, underappreciated
335 threat to wildlife far beyond the burn extent, with reports indicating a capacity to impact animal
336 behavior (19) and human health (42). Nevertheless, focusing on coarse trends in taxa belies complex

337 species-specific responses. For example, fire in the wider landscape seemingly benefitted
338 herbivorous mammals within our study timeframe (Fig. S6), presumably due to increased foraging
339 opportunities, but these effects were reversed when all mammals were aggregated into a single
340 taxonomic unit (Fig. 3).

341 Fire impacts are mediated by the discrepancy between historical and current fire regimes (6),
342 amplifying concerns over the proliferation of fire activity in many tropical regions in recent decades (3,
343 25). This concern is mirrored on Bornean peatlands, where analysis of peat cores indicates that fire
344 has been a rare phenomenon over most of the last 30,000 years, but has increased markedly in
345 recent centuries alongside an increased human presence in the region (43, 44). Our time-series
346 analyses demonstrate that increases in the frequency and intensity of burn events within the wider
347 landscape are associated with the deterioration of plant phenological processes, water quality and
348 biodiversity in forest areas. Moreover, these ecological impacts were most pronounced in the
349 aftermath of megafire events. Studies in the Amazon have shown that recurrent, high intensity fires
350 amplify the structural and compositional downgrading associated with burn events (16), exacerbating
351 downstream effects on ecosystem processes and wildlife persistence (6, 11). For example, we found
352 that indirect fire impacts were particularly acute for threatened vertebrates, contributing towards
353 broader concerns that uncontrolled megafires may elevate the risk of species extinctions, even
354 beyond the burn extent (45). While we observed ecosystem properties in forest areas to be able to
355 recover quickly to pre-disturbance levels following megafires in the broader study landscape in
356 Borneo, biodiversity in the Amazon has been shown to experience a gradual erosion following fire,
357 with potentially long-term consequences for wildlife-mediated processes underpinning habitat
358 recovery (20). Taken together, these results indicate that fire management should actively prioritize
359 tropical peatland areas that frequently burn, to minimise the risk of intense fires over time and prevent
360 irreversible state shifts.

361

362 *Post-fire recovery*

363 Ecological recovery of tropical forest following fire is largely determined by the retention of large
364 reproductive trees and seedling recruitment (46). Based on these criteria, our study provides a mixed
365 prognosis for natural post-fire recovery in tropical peatlands. On the one hand, the sustained absence
366 of large trees is known to cause deficits in seed production for native species (46), manifesting in our

367 case as a sustained decline in non-pioneer tree diversity across the 12-year regeneration time-frame
368 studied. On the other hand, our results provide some evidence of compositional recovery, with some
369 ecosystem (e.g., canopy height) and biodiversity (e.g., damselflies) components at least partially
370 recovering over relatively short time-frames. Light-demanding pioneer vegetation also became less
371 prevalent over time, resulting in increased seedling recruitment, with sustained growth indicated by
372 concomitant increases in sapling density. Given that immature trees are extremely vulnerable to fire-
373 related mortality, including in wetland forest areas such as the Pantanal (47), the extent to which this
374 recovery can be maintained will be dictated by the capacity of each peatland to resist future fire.

375 The demonstrated links between habitat structure, microclimate and biodiversity limit the
376 ability of vegetation and wildlife to rebound from fire within our 12-year study period, particularly for
377 forest specialist species. However, it is reasonable to expect fuller recovery of biodiversity over
378 decadal or centennial timeframes. For example, we found higher seedling and sapling densities in old
379 compared to new burned areas, which over longer time periods and in the absence of repeated fire,
380 should lead to increased density of large fruiting trees, providing resources for frugivores to return.
381 Indeed, in nearby areas on Borneo, recovery of tropical peatland tree diversity was possible two to
382 three decades after fire, though even relatively infrequent repeated fire (50-100 year interval) may
383 substantially suppress recovery (28). Paleoecological evidence indicates an ability for plant
384 communities to persist following fire several thousand to several hundred years ago, while also
385 revealing declines in peat-swamp forest and an apparent lack of regeneration associated with more
386 recent increased anthropogenic influence and fire incidence (43, 44). Our data illustrate the sustained
387 decline of forest-specialist tree species up to 12 years following fire, emphasising that full recovery of
388 species diversity following fire is likely to be a slow process. In turn, this reiterates the need for fire
389 management to be considered an integral part of tropical peatland protection, restoration and
390 revegetation efforts (31).

391

392 *Managing tropical landscapes for fire*

393 Despite the importance of appropriate management strategies to safeguard fire-sensitive ecosystems,
394 efforts to suppress forest fires often have limited success (10). Furthermore, it is becoming
395 increasingly recognized that positive ecological and social outcomes arise from integrated policies
396 that prioritize fire prevention and habitat restoration concurrently (31, 48). In tropical regions, most

397 fires are of anthropogenic origin (2), therefore policy mechanisms that limit fire use in agriculture and
398 tackle deforestation, such as Indonesia's 2011 moratorium on forest and peatland conversion, are
399 fundamental. Policy can be strengthened further by augmenting preventative management with
400 restoration actions to prevent recurring fire and arrested succession arising from feedback loops. We
401 demonstrate that post-fire recovery in tropical peatland is a gradual process and areas subjected to
402 frequent/intense fires may not fully recover unassisted, at least across human relevant timeframes
403 (22). For example, across Borneo, over 2.5 million hectares of peatland have persisted in a fern-
404 dominated state for nearly 20 years (49).

405 Restoring the water table of degraded peatlands is a critical first step to prevent future fires,
406 though efforts to block drainage canals dug for agricultural conversion or timber extraction may in
407 some cases lack community support (31, 50, 51). Further interventions may be required to remove
408 biophysical barriers to succession and enhance vegetation diversity. For example, natural regrowth
409 can be supplemented with cost-effective direct seeding of native species from adjacent unburned
410 forest (52), and recent syntheses provide a valuable knowledge base for increasing the success of
411 active tree planting to revegetate burned tropical peatland areas (53). Moreover, identifying and
412 maintaining connected areas of unburned habitat ("fire refugia") can provide a source of seeds, while
413 also reintroducing vertebrate-mediated processes to fire-affected areas (54). We present a pathway to
414 fire prevention and restoration in forested tropical habitats, with an emphasis on peatlands, but it is
415 also important to acknowledge that fire management must be an adaptive process tailored to the
416 socio-ecological context. A one-size fits all approach is therefore unlikely to be effective.

417 An important first step in such an adaptive process is to develop a detailed understanding of
418 how fire impacts forest ecosystems, the specific aspects of the fire regime driving ecological
419 disruption and the potential for natural recovery. Here, we find that forested tropical ecosystems are
420 highly vulnerable to recurrent, high-intensity fires, and demonstrate that fire-affected ecosystems are
421 capable of natural recovery, but assert that management actions may be required to break fire
422 feedback loops and prevent arrested succession. Capitalizing on lessons learned here and elsewhere
423 in the tropics ((6, 24), and interpreting these across a range of socio-ecological contexts, will be
424 critical in reducing the prevalence of uncontrolled forest fires and mitigating their impacts across the
425 tropical realm.

426

427 **Materials and Methods**

428

429 *Study site*

430 Field data were collected in the Natural Laboratory of Peat-Swamp Forest (NLPSF) special research
431 zone within the Sebangau National Park, Central Kalimantan, Indonesia (Fig. 1). The area comprises
432 ombrogenous mixed peat-swamp forest with peat depth ranging from 0.4 to 2.6 m (55) and
433 experienced 40 years of logging prior to formal protection in 2004 (56). Timber-extraction canals
434 (typically 1-2 m wide and 0.3-1.3 m deep) remain, however, causing continued peat drainage and
435 heightened fire risk (51). Despite high annual rainfall (~3,000 mm) and ongoing hydrological
436 restoration efforts, parts of the forest have therefore burned intermittently, creating a mosaic of
437 predominantly unburned forest interspersed with areas burned at different times. The site is bordered
438 in the north by the blackwater Sebangau River, which originates in the swamp and runs for ~150 km,
439 before discharging into the Java Sea (35). No human settlements are present within the field data
440 collection area, though the village of Kereng Bangkirai (population ~5,500) is situated ~2.5 km distant.

441

442 *Characterizing spatio-temporal fire regimes*

443 We developed a historical profile of fire regimes across Central Kalimantan between November 2000
444 and January 2020 using fire detection data obtained from the Moderate Resolution Imaging
445 Spectroradiometer (MODIS) thermal anomalies MCD14ML product Collection 6. These data
446 correspond well with ground-truthed burned areas in tropical peatlands (57). Detection data
447 comprised the date, time, location and frequency of active fires at 1 km spatial resolution, plus
448 ancillary information on fire intensity (radiative power) and detection confidence. To avoid false
449 detections resulting from non-fire heat signatures, we excluded low confidence thermal anomalies (<
450 30%; (25)). The resulting dataset comprised 235,600 fire detections across the 20-year period, with
451 90% of observations concentrated within a distinct fire season corresponding to late dry season
452 (August-October), which may be extended by a month or more during drought-affected years
453 associated with El Niño events. We defined megafire periods as months with statistically anomalous
454 fire activity at both provincial (Central Kalimantan: 153,564 km²; human population 2.4 million) and
455 local scales (NLPSF boundary augmented with a 25 km buffer; total area: 625 km²; human population

456 ~146,000). This resulted in six megafire events, which matched well with other reports of major fire
457 events in the region (23). Full details of this procedure are provided in Appendix S1.

458

459 *Field data collection*

460 To assess direct fire impacts, we compiled fire treatment datasets for 27 ecological components
461 across 181 sampling locations between April 2017 and September 2021 (Table S1), representing
462 areas affected by a recent major burn event in 2015 (“new burn”; $N=72$) and those recovering from
463 fires up to and including 2006 (“old burn”; $N=27$). Burn treatments therefore captured immediate fire
464 impacts and the potential for recovery in burned areas. For comparison, baseline data were also
465 collected from forest areas with no history of fire (“unburned”; $N=82$). Datasets were not all collected
466 across all sampling locations, or at the same time, producing variation in sample sizes and post-fire
467 intervals between treatments.

468 To explore temporal variation in peatland ecosystem dynamics relative to fire regimes within
469 the landscape, we compiled ecological time-series datasets spanning a 16-year period (September
470 2003-December 2019; Table S1; Appendix S2). This timeframe captures variations in annual fire
471 regimes typical of the region, including multiple megafire events. Time-series datasets encompassed
472 578 temporally-replicated surveys across 236 sampling locations for nine ecological components
473 (Table S1). All datasets coincided with at least two megafire events, but sampled different locations
474 and timeframes within the 16-year temporal window. Full methodological details for all fire treatment
475 and time-series datasets listed in Table S1 are provided in Appendix S2.

476

477 *Modelling framework*

478 *Direct impacts of fire and the potential for post-fire recovery*

479 Fire treatment data for ecological components were summarized as mean values across sampling
480 locations. In contrast, temperature data were calculated as maximum daily values, to capture
481 microclimatic extremes that may compromise environmental suitability for vegetation and wildlife.
482 Biodiversity characteristics were expressed as species counts and abundance estimates, averaged
483 across temporal replicates where applicable, to evaluate compositional and population-level variability
484 across treatments. Species richness estimates were bias-corrected for uneven survey effort using
485 sample-based extrapolation (Appendix S4.1.1; (58)).

486 We developed pairwise comparisons of ecological components in burn treatments relative to
487 “unburned” forest controls, using standardized mean differences (Hedges g), modified to account for
488 heteroscedasticity between treatments (Appendix S4.1.2). This measure accounted for variation in
489 sample sizes and reconciled different measurement units between datasets. To account for non-
490 independence among effect sizes for datasets with multiple treatment groups (i.e. containing both
491 new and old burn conditions), sample sizes in burned forest were adjusted by dividing them by the
492 number of times controls were compared with burn treatments (59). For consistency among datasets,
493 negative effect sizes represented detrimental impacts of fire on peatland ecosystems, while positive
494 effect sizes conveyed ecological benefits of fire (Appendix S4.1.2).

495 To examine the relative consequences of fires on peatland ecosystems, we summarized
496 effect sizes using a hierarchical mixed effects meta-analysis. This framework controlled for higher
497 precision in datasets containing a greater number of statistical replicates. We specified random
498 effects for: data type (i.e., ecosystem property or biodiversity), to understand coarse-scale ecological
499 responses to fire; ecological components, to assess fire impacts on specific aspects of peatland
500 ecosystems; and individual observations, to explicitly model residual variance. We quantified overall
501 fire impacts on peatland ecosystems by weighting dataset-specific effect sizes by the inverse of their
502 variance, plus the inter-dataset variance (60).

503 To quantify proportional changes in each ecological component, we constructed generalized
504 linear mixed-effects models (GLMMs). GLMMs were selected because they extend traditional linear
505 regression frameworks to accommodate data types common to ecological assessments (counts,
506 proportions). All models were specified as mean parameterizations describing each component as a

507 linear function of fire treatments. We also included a spatial random effect to account for clustered
508 sampling where necessary. Proportional changes between unburned controls and burn treatments
509 were calculated post-hoc using the formula: $((\alpha_{\text{burned}} - \alpha_{\text{unburned}}) / \alpha_{\text{unburned}}) \cdot 100$, where α represents
510 model-estimated treatment means. See Appendix S4.2 for further details on GLMM specification.

511

512 *Indirect fire impacts: Temporal variation in ecosystem properties and biodiversity relative to megafire*
513 *regimes*

514 Prior to modelling, time-series datasets were partitioned into discrete primary sampling occasions,
515 termed sampling seasons, based on a combination of sampling frequency, life history characteristics
516 and meaningful periods of fire activity (3-months for terrestrial vertebrates; 1-month for all other
517 ecological components). Across all datasets, seasons operated consecutively to provide complete
518 temporal coverage across the data collection period. For biodiversity datasets, we constructed
519 species-specific detection histories for each taxonomic group by pooling detection/non-detection data
520 into discrete sampling occasions nested within seasons. Full details of time-series data processing
521 are provided in Appendix S4.3.

522 To build a temporal profile of fire regimes for each time-series dataset, we extracted seasonal
523 summaries of fire frequency and intensity (fire radiative power: mean, max, standard deviation, sum)
524 from fire detection data. Due to high levels of collinearity between intensity metrics ($|r| > 0.7$; $VIF > 5$),
525 we selected the sum of fire radiative power to represent this aspect of the fire regime, as it
526 consistently outperformed competing measures during bivariate exploratory analysis (Table S2). To
527 estimate the extent to which megafire impacts radiate across space and time, we calculated the time
528 since last megafire (months) and Euclidean distance (km) from all fire detections occurring within the
529 previous megafire period for each sampling location. Throughout, we extract covariates across buffer
530 radii selected using scale optimization methods (Table S2). This approach addressed considerable
531 uncertainty regarding the appropriate scale of effect for fire impacts (61), which has been shown to
532 extend in excess of 3 km for certain taxa (62). All fire covariates were centered around their mean
533 values and scaled to one-unit standard deviation to place them on a comparable scale and improve
534 computational efficiency.

535 We implemented GLMMs to quantify temporal trends in ecosystem properties against the
536 backdrop of megafire events. GLMMs were selected due to their capacity to incorporate random

537 effect structures that compensate for non-independence in temporal assessments arising from repeat
538 observations at the same sampling location. Annual trends in ecosystem properties were estimated
539 using season-specific random intercepts. We also incorporated a spatial random effect to account for
540 spatially-structured variation due to unobserved ecological factors.

541 To examine biodiversity responses, we employed hierarchical multispecies occupancy
542 models to provide inference at multiple taxonomic levels, improve estimation precision for infrequently
543 observed species and explicitly account for imperfect detection (63). We described the occurrence
544 state (the true presence/absence of a species) on the logit scale using season-specific intercepts and
545 spatial random effects terms. We introduced a random walk prior to the random occupancy intercepts
546 to improve estimation precision by allowing the sharing of information between consecutive seasons
547 (following (64)). We described the detection process on the logit scale, using a season-specific
548 intercept and a measure of survey effort to address differences in sampling intensity between
549 seasons. We summarized temporal trends by taxon, IUCN threat status (ground-dwelling
550 birds/mammals), ecologically meaningful groups (mammals: feeding guilds), commercial value (fish
551 only, based on data from (38, 51)) and species. Details of group assignment are presented in Table
552 S3.

553 Building on this model structure, we constructed a further two candidate models for each
554 time-series dataset to understand the specific aspects of fire regimes driving temporal trends: 1) a fire
555 properties model, to capture the additive effects of fire frequency and intensity; and 2) a spatio-
556 temporal proximity model, to understand how distance in space and time mediates megafire impacts.
557 Across all models, we incorporated quadratic terms where appropriate to model non-linear
558 associations. To provide quantitative comparisons between candidate models, we calculated
559 Wantanabe-Akaike Information Criterion (WAIC), which is a within-sample model selection criterion,
560 robust to statistical frameworks containing latent parameters. Throughout, we considered models with
561 $\Delta\text{WAIC} < 2$ to have comparable statistical support and $2 < \Delta\text{WAIC} < 8$ to have moderate support
562 (Appendix S4, Table S4).

563 All analyses conducted were specified within a Bayesian framework, implemented in rstan
564 (hierarchical mixed-effects meta-analysis) and JAGS (all GLMMs and occupancy models) called
565 through R version 4.0.2. Model development, structure, specification and evaluation details are
566 presented in Appendix S4.

567

568 *Data Availability*

569 Data associated with this manuscript are available for download from the UK CEH Environmental
570 Information Data Centre ([hyperlink/DOI to be added to final version](#)).

571

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573

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589

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752 **Figure 1:** Map of study site, illustrating survey locations within Sebangau National Park and on
753 Borneo (a); and at relevant spatial scales (b-d). The study area is centered around 2°19'00" S and
754 113°54'29" E and comprises low-lying (5-25 masl), ombrogenous peat-swamp forest. Parts of the
755 forest have burned intermittently, creating a mosaic of predominantly unburned forest interspersed
756 with areas burned at different times. For surveys conducted using transects, points indicate the
757 central location of the transect. Central butterfly survey locations indicated in (b) refer to indirect, time-
758 series data collection locations, whereas those in (d) indicate locations for direct comparisons of
759 burned and control conditions. Fish sampling was conducted along the Sebangau River (average
760 water body width 30 m and depth 5.4 m around our survey locations; (51)). See Table S1 and
761 Appendix S2 for methodological and sample size details for all datasets. Map data sources: forest
762 cover (65); burned areas extracted from dNBR1 Landsat imagery (Landsat-8 OLI/TIRS image courtesy
763 of the U.S. Geological Survey) and (66); rivers and conservation areas courtesy of Indonesian
764 Geospatial Agency (SIGAP KLHK).

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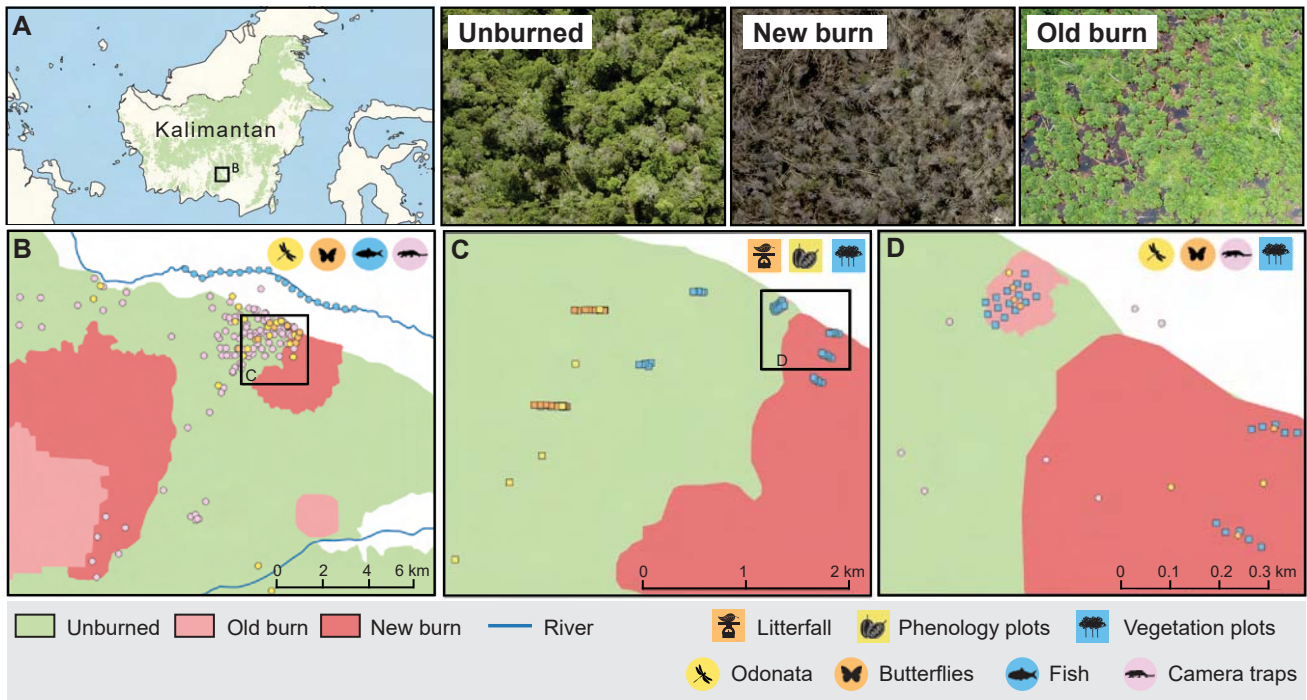
766 **Figure 2:** Percent change of ecosystem properties (top to bottom: maximum daily temperature,
767 grass/fern/canopy cover, pitcher/pandan/liana.seedling/sapling/tree density, canopy height and
768 aboveground biomass),and biodiversity characteristics (top to bottom: species richness and
769 abundance of trees/dragonflies/damselflies/butterflies/amphibians/reptiles, Acoustic Complexity Index,
770 Acoustic Diversity Index, Bioacoustic Index, Normalized Difference Soundscape Index) in burn
771 treatments relative to unburned forest controls (vertical dashed black line). Burn treatments captured
772 “new burn” areas subjected to a recent fire event in 2015 (red hues) and “old burn” areas recovering
773 from fire activity dating back to 2006 (orange hues). Uncertainty is expressed using 75% Bayesian
774 Credible Intervals (BCI; thick black horizontal lines) and 95% BCI (thin black horizontal lines). The
775 three asterisks denote ecological components that exceeded 100% increases in burn treatments
776 relative to unburned forest controls and for which BCI lines are therefore not visible: fern cover:
777 1156% increase in new burn treatment (95% BCI: 910-1464%); pitcher plants: 954% increase in old
778 burn treatment (95% BCI: 639-1390%) dragonflies: 290% increase in abundance in old burn
779 treatment (95% BCI: 98-606%).

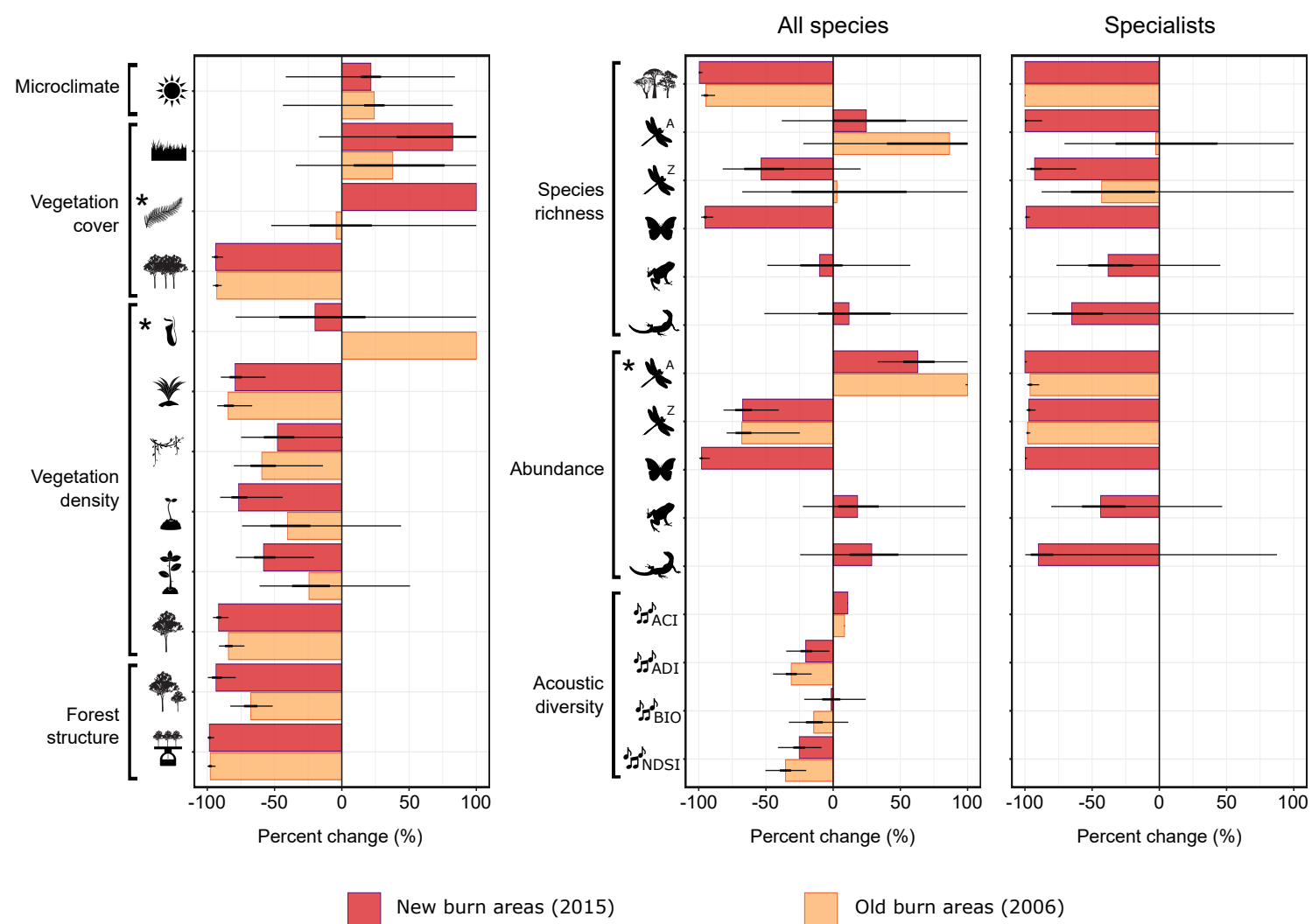
780

781 **Figure 3:**Temporal trends (blue lines) demonstrated by ecosystem properties (left panel; top to
782 bottom: fire frequency, river pH, leaf-fall, leaf/flower/fruit expression) and biodiversity (all species, right
783 panel; occupancy of butterflies, fish, ground-dwelling birds, medium-large terrestrial mammals, IUCN-
784 threatened vertebrates, commercially valuable fish) in response to multiple megafire events (red
785 vertical lines) across a 16-year timeframe (January 2004 to January 2020). Throughout, occupancy
786 reflects the probability that the species is present in the study landscape, where a value of zero
787 indicates that the species is completely absent during and a value of one confirms that the species
788 was present during the observed timepoint. We present temporal summaries as posterior means of
789 season-specific intercept terms (hollow blue points) and express uncertainty using 95% Bayesian
790 Credible Intervals (gray ribbons). Trends for forest specialist species are illustrated in Fig. S4.

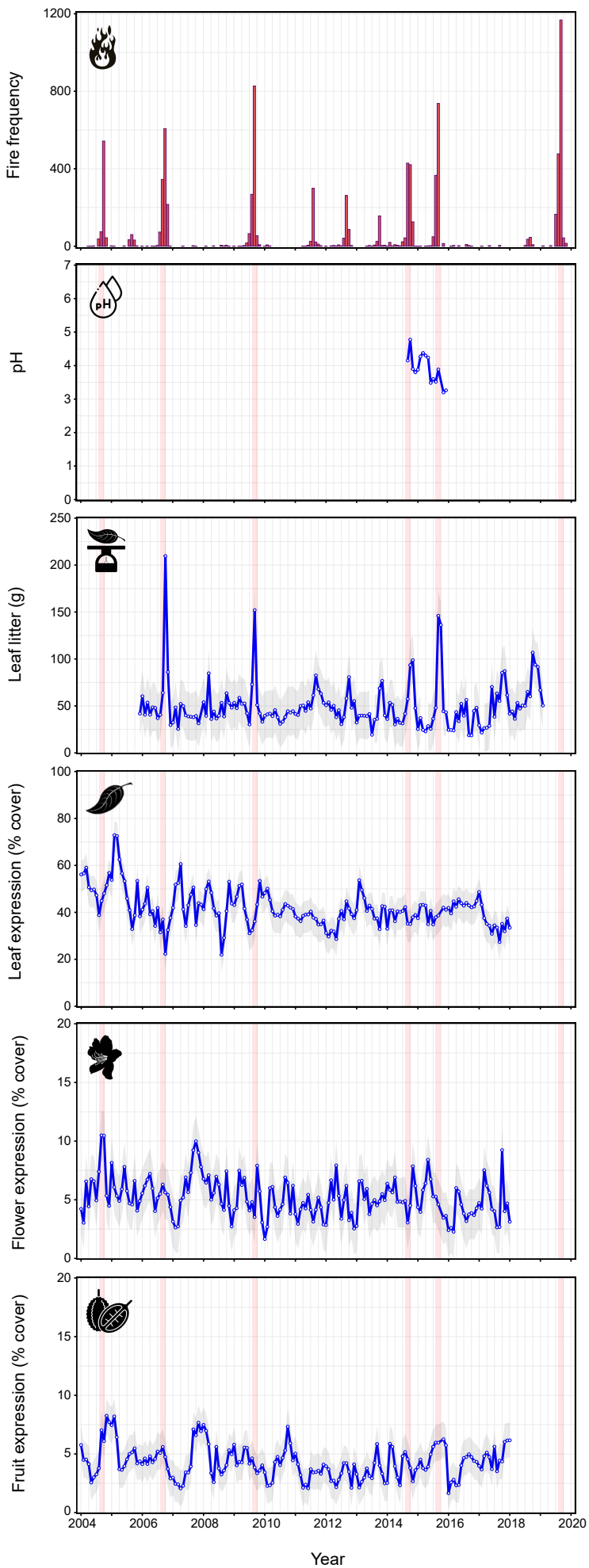
791

792 **Figure 4:** (a) Ecosystem properties and (b) biodiversity responses to fire properties (fire frequency,
793 fire radiative power) and the spatiotemporal proximity to extreme thermal events (distance from
794 megafire, time since last megafire). Occupancy reflects the probability that the species is present in
795 the study landscape, where a value of zero indicates that the species is completely absent during and
796 a value of one confirms that the species was present during the observed time point. Solid blue lines
797 denote the mean of the posterior distribution while grey ribbons denote uncertainty, expressed using
798 95% Bayesian Credible Intervals. Non-influential parameters are presented in light gray. For definition
799 of symbols, see Figure 3. Trends for forest specialist species are illustrated in Fig. S5.

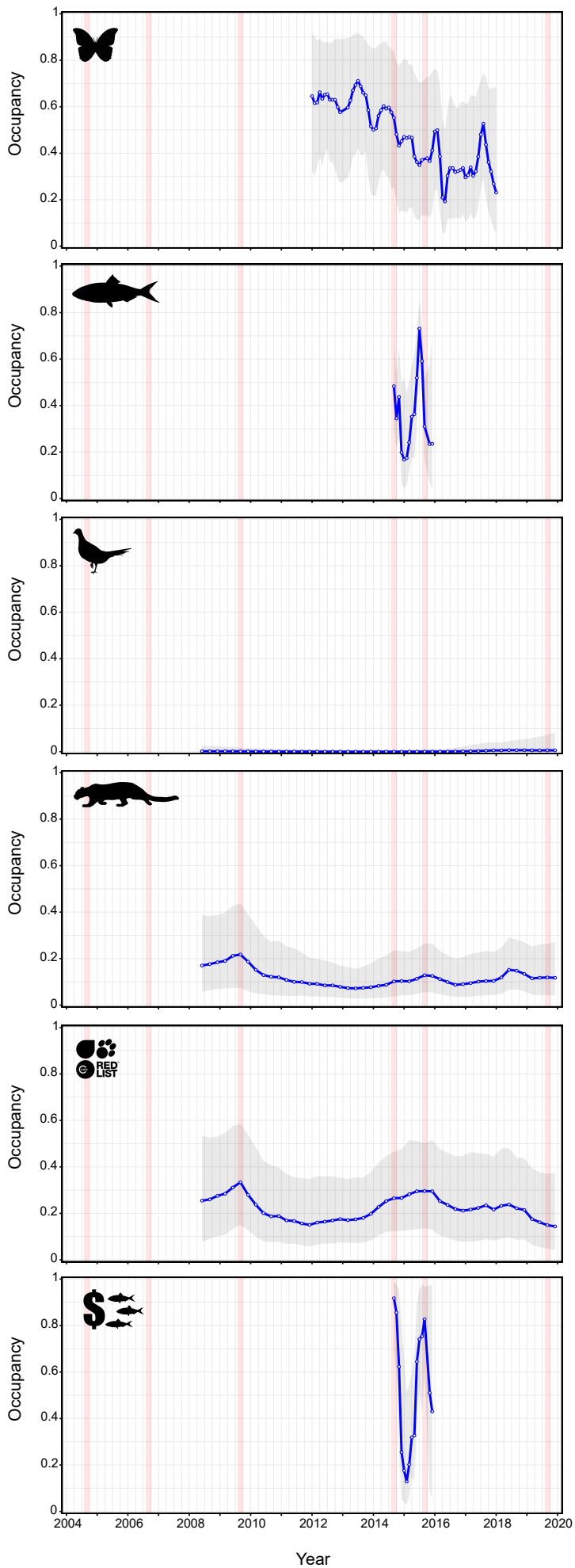




Ecosystem properties

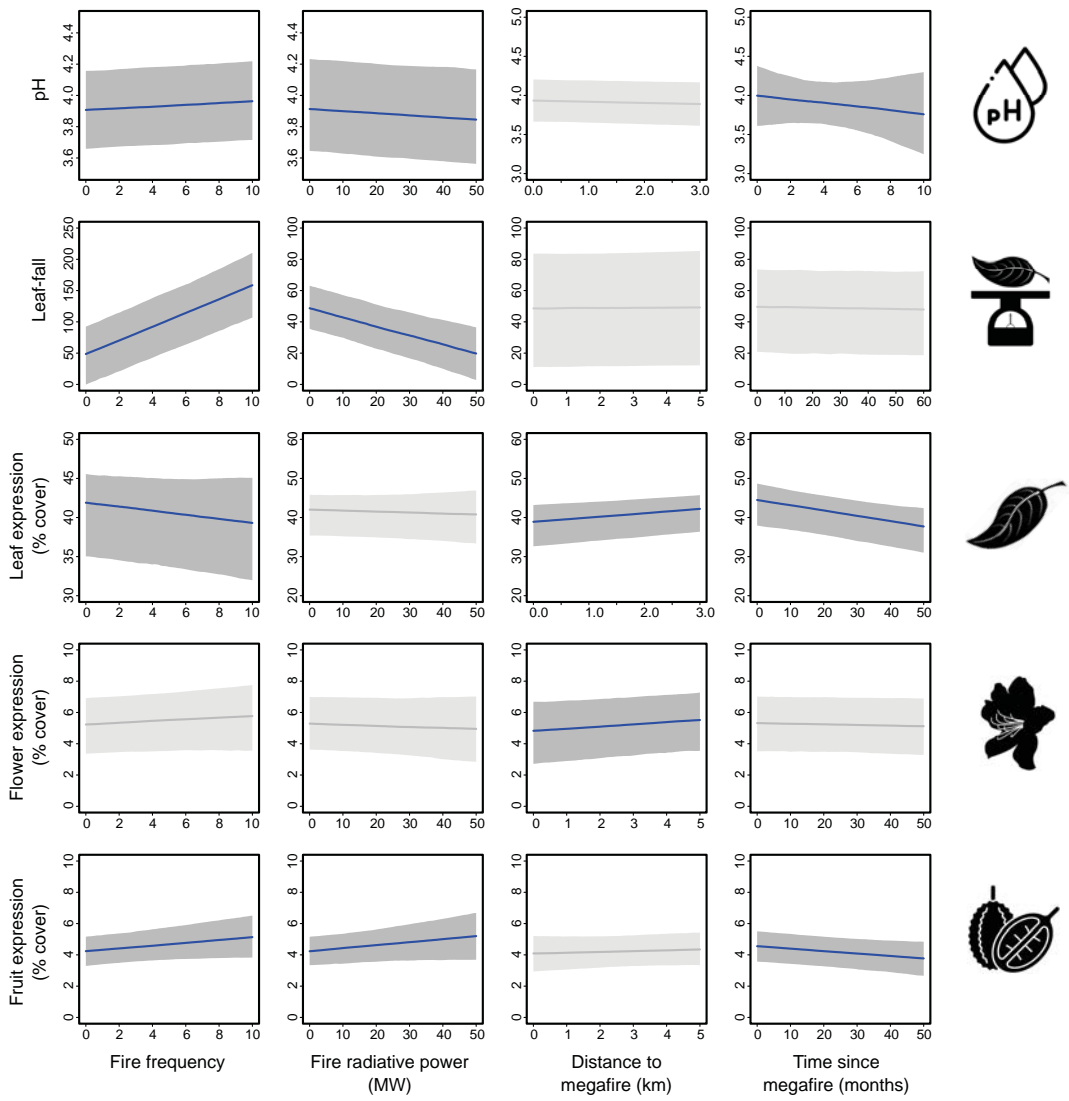


Biodiversity



(a)

Ecosystem properties



(b)

Biodiversity

