Optimizing landscape-scale monitoring programmes to detect the effects of megafires

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Abstract

Aim: By virtue of their spatial extent, landscape-scale monitoring programmes may be well-suited to support before-after/control-impact (BACI) studies of major disturbances such as megafires, but they may only have a few affected sites, reducing statistical power. I tested whether a variety of hypothetical but logistically plausible survey designs could provide statistically powerful assessments of hypothetical but empirically based population responses to megafire.

Location: Simulation focused on fire-prone forests.

Methods: I varied the number of affected sites, detection probability, baseline occupancy and species’ responses to fire to create 72 monitoring scenarios. I then simulated 10 years of site occupancy data in which a megafire or other disturbance occurred between years 5 and 6 (n = 500 iterations).

Results: Statistical power to correctly reject the null hypothesis of no population response to megafire was high (mean across all scenarios = 0.78), but power to identify the correct population response (e.g. post-fire occupancy declined and then recovered) was low (mean = 0.29). Statistical power to not underestimate the effect of a megafire on site occupancy was fairly high (mean = 0.66), but power to accurately estimate site occupancy was low (mean = 0.25). Statistical power increased with the number of affected sites (i.e., sample size) and with the intensity of the focal species’ response to megafire. Case study simulations based on an existing acoustic monitoring programme in the Sierra Nevada, USA, indicate that it is likely to identify Spotted Owl and Black-backed Woodpecker population responses to megafires. Researchers can use the included simulation tutorial to implement their own power analyses.

Main conclusions: Landscape-scale monitoring programmes can identify population changes following megafires, but cannot reliably produce nuanced results, especially with only five years of post-fire data. Smaller-bodied species, which could be studied at more sites, are likely to be better focal species for megafire BACI studies. Aggregating landscape-scale studies’ sampling coverage across many fire footprints to study the overall effects of megafires—rather than the effects of individual fires—may be a more informative approach.
1 | INTRODUCTION

From climate change to species range shifts, ecological processes are occurring at increasingly extensive spatial scales. The occurrence of megafires—atypically large and severe fires—is one such process, and a combination of climate change and both historical and contemporary land use is making them more common in dry forests in North America (Miller et al., 2009; Stevens et al., 2017; Westerling, 2016), eastern Australia (Boer et al., 2020) and the Amazon (Fidelis et al., 2018). These changing fire regimes increase the risk of lasting forest conversion reinforced by positive feedback loops (Coop et al., 2020). In regions where vast swaths of land are managed by single entities, management decisions made in response to the growing risk of megafires can also have sweeping ecological ramifications (Wood & Jones, 2019). However, the direct effects of megafires on wildlife populations can be difficult to discern because most studies to date have been conducted opportunistically after fires have occurred.

By virtue of their spatial extent, landscape-scale monitoring programmes should be well-suited to provide survey coverage within the footprints of future megafires, potentially allowing for before-after/control-impact (BACI) studies. Data from camera traps, hair snares and autonomous recording units (ARUs) collected at landscape scales can support statistically powerful multispecies occupancy and mark–recapture analyses to assess population trends (Banner et al., 2018; Ellis et al., 2014; Magoun et al., 2011; Steenweg et al., 2016; Wood et al., 2021; Wood et al., 2019). However, the statistical power of these types of non-invasive monitoring programmes has primarily been evaluated in the context of population trends affecting many or all sites, rather than the effects of localized disturbances (e.g., Banner et al., 2019; Ellis et al., 2014; Steenweg et al., 2016; Wood et al., 2019).

Ironically, compelling demonstrations of the effects of megafires on threatened species have actually come from small- to moderate-scale studies. In the Sierra Nevada, USA, the 2014 King Fire burned 30 of 45 Spotted Owl (Strix occidentalis) territories in a ~ 350-km² study area in which marked individuals had been censused annually, enabling an elegant BACI study with which researchers showed conclusively that large, severe fires drastically reduce Spotted Owl territory occupancy and increase territory extinction (Jones et al., 2016). The 2013 Rim Fire also in the Sierra Nevada had a contrasting effect on an unmarked population of Great Gray Owls (S. nebulosa) that had been surveyed for 10 years before the fire, with territory occupancy remaining high for three years post-fire (Siegel et al., 2019). In south-eastern Australia, three years of pre-fire data and four years of post-fire data revealed that the 2009 Black Saturday fire complex (720 km²) caused 12 of 13 bird species to decline in response to the amount of severely burned forest on the landscape (Lindenmayer et al., 2014). The overlap of megafires with longer-term, smaller-scale studies circumvented a fundamental trade-off monitoring programmes face between survey intensity and spatial extent, but such events are unlikely.

Resource and logistical constraints dictate that landscape-scale monitoring programmes survey only a fraction of the landscape; consequently, the number of survey sites within the footprint of any given megafire may be low. For example, a landscape-scale acoustic monitoring programme designed for Spotted Owls in the Sierra Nevada initiated after the King Fire (Wood et al., 2019) would have included just 8–10 owl territory-sized sites within the footprint of the King Fire, as opposed to the 30 owl territories that were surveyed by Jones et al., (2016). Precision and statistical power improve with the number of survey sites (Ellis et al., 2014; Steenweg et al., 2016; Wood et al., 2019), so if a megafire were to overlap the footprint of such a monitoring programme, its ability to deliver critical information—such as whether endangered species’ populations suffered as a result of the fire—could be limited.

Landscape-scale monitoring is incipient or ongoing for a variety of species in fire-prone regions. The Spotted Owl, which is negatively affected by megafires (Jones et al., 2016; Rockweit et al., 2017), is the focal species of passive acoustic surveys across the Sierra Nevada and Pacific north-west (Duchac et al., 2020; Wood et al., 2019). Bats, which may also be negatively affected by megafires (Jung, 2020), are subject to acoustic monitoring across the Pacific Northwest (Rodhouse et al., 2019). Carnivores such as fisher (Pekania pennanti) and marten (Martes americana) are monitored in the Sierra Nevada (Zielinski et al., 2013), and wolverines (Gulo gulo) and grizzly bears (Ursus arctos) are monitored in the northern Rocky Mountains (Ellis et al., 2014; Steenweg et al., 2016). Camera traps are used extensively to assess invasive carnivore removals across Australia, and such data could also be leveraged to conduct megafire-related monitoring (Comer et al., 2020; Robley et al., 2014). Importantly, the legal protections and public prominence of some species already subject to landscape-scale monitoring confer to them considerable influence on forest management policy. Therefore, accurately measuring the effects of megafires on such species—like the Spotted Owl—will have direct bearing on forest restoration, the provisioning of ecosystem services, and human health and safety across fire-prone landscapes (Wood & Jones, 2019).

I hypothesized that the ability of landscape-scale monitoring efforts to provide insight into wildlife responses to megafires depended on the number of survey sites affected and focal species’ seasonal detection probability, baseline prevalence and responses to disturbance (Ellis et al., 2014; Southwell et al., 2019; Steenweg et al., 2016; Wood et al., 2019). I simulated logistically plausible survey designs and ecologically realistic responses to large, severe fires to determine whether hypothetical landscape-scale monitoring...
programmes may be capable of detecting population changes caused by megafires or other large-scale disturbances that affect focal species’ habitat suitability. I predicted that statistical power would increase with the number of affected sites and that power would be higher for more pronounced changes (e.g., a severe decline in a common species or a rapid increase in a rare species). No aspect of the simulation was taxon- or ecosystem-specific; the results are applicable to any case in which the detection probability, baseline occupancy and response to disturbance are similar to the values used here. Moreover, the simulation tutorial is freely available so that researchers can conduct customized power analyses based on their needs (Supporting information). Wildfires with atypically large and homogeneous patches of severely burned areas are increasingly common (Miller et al., 2009; Stevens et al., 2017; Wintle et al., 2020), so understanding whether landscape-scale monitoring programmes are capable of identifying subsequent population changes is increasingly important for conservation.

2 | METHODS

2.1 | Hypothetical monitoring designs and population baselines

I simulated 10 years of site occupancy data for eight hypothetical survey designs in which a high-severity fire or other disturbance occurred between years 5 \((t_5)\) and 6 \((t_6)\).

Either seven, 15, 30 or 60 monitoring sites were affected, which reflects a range of possibilities that depend on the size of the disturbance and the density of survey sites on the landscape, which itself may vary within a study (e.g. ARUs may be co-deployed and their results pooled for species with large home ranges, such as Spotted Owls, but analysed independently for other species, like most passerines). Simulating seasonal detection probability \(p^*\); the probability of detecting a species over the course of the sampling season) simplified the simulation by reducing two dimensions, detection probability \(p\) and the number of secondary sampling periods \(n\) into a single number \(p^* = 1 - (1 - p)^n\), though both can be modified in the code. Limiting the occurrence of the fire to between years 5 and 6 had two important benefits. First, it made pre-fire occupancy less sensitive to stochastic changes, which was particularly important when sample size was low. Second, it reflected the importance of timely information when implementing adaptive management.

While ten or more years of post-fire data would yield higher statistical power (Banner et al., 2019), it would also delay management responses in an era when ecosystem change is unfolding very rapidly. The included power analysis tutorial explains how users can extend the post-fire period to as many years as desired.

For each of the eight hypothetical study designs, I considered nine types of populations in which a hypothetical species had a realistic prevalence on the landscape and a plausible response to a megafire. Initial site occupancy \(\psi\) could be 0.25, 0.5 or 0.75, which encompasses occupancy rates reported for most Sierra Nevada passerines for which point counts have been a viable survey technique (Table S2 of Tingley et al., 2009) and two species of bat in the Pacific Northwest (Rodhouse et al., 2019). It is also consistent with species relevant to the management of fire-prone forests: Spotted Owl site occupancy in the northern Sierra Nevada is approximately 0.53 (Wood et al., 2020), fisher site occupancy in the southern Sierra Nevada is 0.26–0.058 depending on the subregion (Zielinski et al., 2013), and Black-backed Woodpecker \((Picoides arcticus)\) site occupancy in the Sierra Nevada can span that entire range of values depending on the time since fire (Tingley et al., 2018). Baseline site extinction \(\epsilon_B\) and site colonization \(\gamma_B\) ranged from 0.05 to 0.13 depending on initial site occupancy such that the control population was stable for the duration of the simulation (Table 1).

2.2 | Hypothetical megafire responses

The three simulated disturbance responses were necessarily general, but resembled the published responses of focal species in fire-prone forests to large, severe fire (Jones et al., 2016; Latif et al., 2016; Tingley et al., 2018). Response 1 was an ephemeral increase in site quality \(\epsilon\) dropped to 0.0 in \(t_6\) and increased linearly to 2\(\epsilon_B\), but in \(t_10\): \(\gamma\) increased to 0.8 in \(t_6\) and decreased linearly back to \(\gamma_B\) in \(t_10\), which represented a post-fire specialist like the Black-backed Woodpecker or Flame Robin \((Petroica phoecea)\) (Lindenmayer et al., 2014; Tingley et al., 2018). Response 2 was an ephemeral reduction in site quality \(\epsilon\) increased to 4\(\epsilon_B\), but in \(t_6\): \(\gamma\) increased to 0.8 in \(t_6\) and decreased linearly back to \(\gamma_B\) in \(t_10\), which represented a species like the Brown Thornbill \((Acanthiza pu-silla)\), which can recover from fires more quickly than most sympatric bird species (Lindenmayer et al., 2014). Response 3 was a permanent,

| Table 1 Simulation parameters and the number of levels in each parameter. Baseline extinction and colonization probabilities were conditional on starting occupancy and were calibrated to yield a stable control population |
| Survey design | Levels |
|----------------|-------|
| Number of affected sites | 7, 15, 30, 60 | 4 |
| Seasonal detection probability | 0.75 or 0.95 | 2 |
| Population attributes | | |
| Initial occupancy (\(\psi\)) | 25%, 50%, or 75% of sites | 3 |
| Baseline pr(extinction) | \((\psi = 0.25) / 0.08 \) or \((\psi = 0.25) / 0.05 \) \((\psi = 0.25)\) | NA |
| Baseline pr(colonization) | \((\psi = 0.25) / 0.08 \) or \((\psi = 0.25) / 0.13 \) \((\psi = 0.25)\) | 6 |
| Post-fire extinction | Dynamic (‐), dynamic (+), permanent (+) | 3 |
| Post-fire colonization | Dynamic (+), dynamic (‐), permanent (‐) | |
severe reduction in site quality (for \( t_{6-10} \), \( \varepsilon \) increased to 0.9; \( \gamma \) decreased to 0.03), which represented a hypothetical old-forest specialist like the Spotted Owl for which some configurations and intensities of fire represent quasi-permanent losses of habitat (Jones et al., 2016). Importantly, these are generalized, hypothetical responses: even “post-fire specialists” like Black-backed Woodpeckers can be negatively affected by fires when patches are extremely large and burn at uniformly high severity (White et al., 2019).

2.3 | Simulation

2.3.1 | General simulations

The eight survey designs and nine population types yielded 72 possible scenarios, each of which I simulated 500 times using Program R 4.0.2 (R Core Development Team, 2020). Each scenario included the impacted sites (i.e., seven, 15, 30 or 60) and four times as many unaffected control sites because increasing the number of control sites increases statistical power in BACI designs (Popescu et al., 2012) and reflects an ideal scenario in which many more unburned sites would be available to serve as a baseline for comparison to the impacted sites. A BACI design would not be possible following a catastrophic event in which most or all sites are burned (e.g. Wintle et al., 2020), and an alternative modelling approach would be necessary.

Occupancy at \( t_1 \) at all sites was a Bernoulli trial based on the given probability of initial occupancy; site occupancy at unaffected sites in subsequent time steps (i.e., \( t_{2-10} \)) was a Bernoulli trial based on the given baseline probabilities of extinction (if the site was occupied at \( t_{t-1} \)) or colonization (if the site was vacant at \( t_{t-1} \)). Site occupancy in impacted sites before the fire was determined in the same matter; after the fire (\( t_{5-10} \), site extinction and colonization probabilities were determined by the response type in that scenario rather than the baseline. This process yielded the true site occupancy for all sites (control and impacted) for all 10 years. Next, I simulated the effect of detection probability: over three secondary sampling periods, detections at occupied sites were Bernoulli trials based on a detection probability (0.37 or 0.54) that yielded the appropriate seasonal detection probability (0.75 or 0.90).

I then formatted the simulated encounter histories for package RMark (Laake, 2013) and implemented three dynamic occupancy models with the \( \psi-\varepsilon \) formulation. Extinction (\( \varepsilon \)) and detection (\( \psi \)) were held constant in all models; the simulated variation in extinction (and colonization) would still be represented as changes in occupancy with the \( \psi-\varepsilon \) formulation. This simplified the modelling process and allowed me to present direct estimates of the more commonly used state variable (\( \psi \), rather than \( \varepsilon \) or \( \gamma \)), rather than derive them from models using the \( \gamma-\varepsilon \) formulation. I compared three models: a null model (three parameters; \( \psi \) is constant across sites and years), a BACI-static model (four parameters; \( \psi_{\text{Burn-stat}} \) allowed post-fire occupancy to differ between burned and control sites) and a BACI-ephemeral model (four parameters; \( \psi_{\text{Burn-eph}} \) allowed post-fire occupancy at burned sites to change linearly with time). I recorded each model’s Akaike information criterion with a correction for small sample size (AICc), occupancy estimates (intercept and \( \hat{p}_{\text{burned}} \), if applicable) and associated standard errors.

2.3.2 | Case study: Sierra Nevada focal species simulations

I conducted another set of simulations using parameters that matched the existing Sierra Nevada acoustic monitoring programme to serve as a case study. I fixed the number of burned sites at 4 and 12, which reflects the survey site density of that programme and its hierarchical design. The landscape is divided into 4 km² hexagonal grid cells, 20% of which are surveyed with two or three ARUs deployed ≥500 m apart (Wood et al., 2019 for further detail). Thus, this scenario represents a 100 km² patch of uniformly high-severity fire. I defined the population attribute parameters to reflect two prominent fire-affected species, Spotted Owls and Black-backed Woodpeckers.

Spotted Owl site occupancy, which would be assessed at four grid cells, and seasonal detection probability under this monitoring programme are 0.43–0.53 and 0.88–0.84, respectively (Wood et al., 2019, 2020), and megafires result in quasi-permanent habitat loss (response 3) (Jones et al., 2016). Black-backed Woodpecker baseline occupancy in the Sierra Nevada region is 0.20 and seasonal detection probability is 0.90–0.93 when vocal lure surveys are used (Tingley et al., 2018). Site occupancy of species would be assessed at the 12 ARUs because their spacing corresponds with comparable surveys (Tingley et al., 2014), and it preferentially colonizes recently burned forests (response 1) (Tingley et al., 2018).

2.4 | Computing statistical power

I measured statistical power in four ways: two based on model selection and two based on occupancy estimates. For the model selection approach, I first tested whether the null model was correctly rejected (\( \Delta \text{AIC}_{\text{Null}} > 0 \)) and then I tested whether the correct model had been identified. In scenarios with responses 1 and 2 (ephemeral increase or decrease in habitat quality), the BACI-ephemeral occupancy model should have the most support (\( \Delta \text{AIC}_{\text{Burn-eph}} = 0 \)); in scenarios with response 3 (a permanent reduction in site quality), the BACI-static model should have the most support (\( \Delta \text{AIC}_{\text{Burn-stat}} = 0 \)).

For the occupancy estimation approach, I compared true occupancy in burned sites to the 85% confidence interval of occupancy at burned sites as estimated by the top model of site occupancy (Arnold, 2010). First, I tested whether the top model underestimated the effect of a megafire on site occupancy. Underestimating the effects of a fire—whether or positive or negative—could lead to insufficient policies that could jeopardize focal species populations, while correctly estimating or overestimating the effects would at worst lead to unnecessarily strict conservation measures that would be unlikely jeopardize a species. In this context, I expressed power
as 1—the underestimation rate. When the population increased in response to fire (response 1), I calculated the overall average number of post-fire years \((n = 5\) years across \(n = 500\) simulations) in which true occupancy at burned sites was greater than the lower 85% confidence interval of estimated occupancy. When the population decreased in response to fire (responses 2 and 3), I calculated the average number of post-fire years in which true occupancy at burned sites was lower than the upper 85% confidence interval of estimated occupancy. Second, I tested whether occupancy had been estimated accurately by calculating the overall average number of post-fire years in which true occupancy at burned sites was within the 85% confidence interval of estimated occupancy.

Finally, I used package `betareg` (Zeileis et al., 2020) to implement four sets of univariate generalized linear models with beta distributions in which the dependent variable was the rate at which (i) any megafire response was detected via model selection, (ii) the correct megafire response was detected via model selection, (iii) the effect of a megafire on site occupancy was not underestimated, or (iv) occupancy was correctly estimated. The number of affected sites, detection probability, baseline occupancy and megafire response type were independent variables. I then compared Efron’s pseudo-\(R^2\) of all models to quantify which aspect of the simulation had the most influence on each of the four metrics of statistical power.

### 2.5 Assumptions and scope of inference

The most fundamental assumption of these power analyses was that the megafire, or, more generically, spatially extensive disturbance, had a uniform effect on focal species habitat suitability in all affected sites. The size and shape of a wildfire, variation in burn severity, post-fire management practices (e.g., salvage logging) and other factors can influence post-fire habitat suitability in complex and interacting ways. A systematic examination of these factors was beyond the scope of this study, but stochasticity of extinction and colonization probabilities among years and sites allowed for some variation. Moreover, large fires that burn at uniformly high severity are increasingly common (Miller et al., 2009; Stevens et al., 2017; Westerling, 2016; Wintle et al., 2020). Thus, it is both important to understand such fires and not unlikely that real fires would generate several or even many sites that are affected very similarly. By November 2020, three separate fires in the Sierra Nevada had burned >650 km\(^2\), and, under the existing Sierra Nevada acoustic monitoring programme (coverage of 20% in a 4 km\(^2\) grid, see 2.3.2), just 14% of such a fire would need to burn at high severity to yield seven affected sites, the fewest considered in these simulations. Alternatively, multiple fires could give rise to the cumulative number of affected sites considered in this study. Thus, the fire considered in these simulations could represent a single high-severity fire or patches of high-severity burns within a larger fire complex.

Detection (\(p\)) remained constant throughout the simulation, indicating the hypothetical focal species’ behaviour (e.g., vocalization rates) and survey device efficacy did not differ between burned and unburned forest, or that monitoring protocols were modified such that more (or less) effort was expended to achieve the same season detection probability (\(p^\star\)).

This approach focuses on the effect of a particular megafire (or patch of high-severity fire, or other spatially extensive disturbance) on a subset of the focal species’ population rather than on the effects of megafires generally on the entire population. The simulated “population response” reflects a localized fluctuation in an otherwise stable population, and ongoing population trends and high interannual variation would challenge the detection of a megafire-driven population decline. However, by improving our understanding of the effects of individual high-severity fires (or patches), such studies improve our capacity to make informed ecosystem management decisions in contexts where such fires are likely to become increasingly common (e.g., Jones et al., 2016).

Finally, the simulations assume that site occupancy is an appropriate method of measuring population change. For territorial resident species such as Spotted Owls, territory occupancy is a reliable proxy for abundance (Tempel & Gutiérrez, 2013); with some data modification, site occupancy may reflect territory occupancy (Wood et al., 2020), but the relationship warrants further exploration. For non-territorial or migratory species, site occupancy may not be the most informative metric of population change because abundance could vary substantially among occupied sites. Fortunately, bioacoustics affords managers some flexibility in changing their state variable (e.g., from occupancy to density Pérez-Granados et al., 2019). For these analyses, however, I focused solely on site occupancy.

### 3 RESULTS

#### 3.1 General simulation results

Statistical power to detect any population response to a megafire via model selection (i.e. \(\Delta AIC_{C Null} > 0\)) was generally high (mean = 0.78, range: 0.42–1.00), but power to identify the correct population response was low (mean = 0.29, range: 0.00–0.61; Table 2). Similarly, statistical power to not underestimate the effect of a megafire on site occupancy was fairly high overall (mean = 0.66, range: 0.46–0.96), but power to correctly estimate site occupancy was low (mean = 0.25, range: 0.05–0.44; Table 2). However, there was substantial variation among scenarios, and results for all 72 scenarios are listed in Table 2, so researchers can identify the scenario most relevant to their study.

Baseline occupancy and seasonal detection probability did not substantially affect statistical power (Table 3). Statistical power to detect a population response was very high (>0.9) when 15 or more sites were affected and when species displayed ephemeral positive or lasting negative responses to megafires (i.e., responses one and three) (Figure 1a; Figure 2a,b; Table 2). The number of affected sites explained 9.6% of the variation in statistical power, and response type explained 52% of the variation (pseudo-\(R^2 = .096\) and
TABLE 2  Complete list of monitoring scenarios with four metrics of statistical power based on 500 iterations of the simulation. Researchers can cross-reference these scenarios with their own projects to estimate their potential statistical power; if none of these scenarios are a sufficient match to a relevant monitoring programme and focal species, a simulation tutorial (Supporting information) can be used to create fully customized power analyses.

| Survey design choices | Population attributes | Model selection | Occupancy estimates | Within 85% CI |
|-----------------------|-----------------------|----------------|---------------------|---------------|
| Affected sites $p^*$ | $\psi_1$ | Response | Null rejected | Correct response | Not underestimated | |
| 7 .37 0.25 1 | 0.998 | 0.002 | 0.692 | 0.385 |
| 7 .37 0.25 2 | 0.410 | 0.230 | 0.533 | 0.277 |
| 7 .37 0.25 3 | 0.584 | 0.532 | 0.668 | 0.084 |
| 7 .37 0.50 1 | 0.902 | 0.098 | 0.590 | 0.234 |
| 7 .37 0.50 2 | 0.386 | 0.242 | 0.449 | 0.394 |
| 7 .37 0.50 3 | 0.892 | 0.630 | 0.700 | 0.104 |
| 7 .37 0.75 1 | 0.726 | 0.274 | 0.371 | 0.174 |
| 7 .37 0.75 2 | 0.378 | 0.204 | 0.357 | 0.394 |
| 7 .37 0.75 3 | 0.980 | 0.732 | 0.742 | 0.078 |
| 7 .54 0.25 1 | 0.986 | 0.014 | 0.656 | 0.368 |
| 7 .54 0.25 2 | 0.354 | 0.202 | 0.568 | 0.278 |
| 7 .54 0.25 3 | 0.544 | 0.446 | 0.728 | 0.086 |
| 7 .54 0.50 1 | 0.914 | 0.086 | 0.590 | 0.269 |
| 7 .54 0.50 2 | 0.412 | 0.268 | 0.479 | 0.388 |
| 7 .54 0.50 3 | 0.860 | 0.526 | 0.766 | 0.116 |
| 7 .54 0.75 1 | 0.746 | 0.254 | 0.387 | 0.196 |
| 7 .54 0.75 2 | 0.432 | 0.256 | 0.400 | 0.405 |
| 7 .54 0.75 3 | 0.952 | 0.610 | 0.800 | 0.105 |
| 15 .37 0.25 1 | 0.996 | 0.004 | 0.687 | 0.409 |
| 15 .37 0.25 2 | 0.454 | 0.344 | 0.531 | 0.381 |
| 15 .37 0.25 3 | 0.660 | 0.358 | 0.684 | 0.168 |
| 15 .37 0.50 1 | 0.946 | 0.054 | 0.777 | 0.200 |
| 15 .37 0.50 2 | 0.436 | 0.336 | 0.532 | 0.379 |
| 15 .37 0.50 3 | 0.966 | 0.524 | 0.703 | 0.150 |
| 15 .37 0.75 1 | 0.896 | 0.104 | 0.608 | 0.286 |
| 15 .37 0.75 2 | 0.416 | 0.308 | 0.466 | 0.395 |
| 15 .37 0.75 3 | 1.000 | 0.606 | 0.659 | 0.135 |
| 15 .54 0.25 1 | 0.990 | 0.010 | 0.628 | 0.355 |
| 15 .54 0.25 2 | 0.484 | 0.358 | 0.536 | 0.398 |
| 15 .54 0.25 3 | 0.696 | 0.276 | 0.727 | 0.179 |
| 15 .54 0.50 1 | 0.942 | 0.058 | 0.702 | 0.248 |
| 15 .54 0.50 2 | 0.572 | 0.440 | 0.503 | 0.437 |
| 15 .54 0.50 3 | 0.954 | 0.352 | 0.742 | 0.189 |
| 15 .54 0.75 1 | 0.914 | 0.086 | 0.602 | 0.324 |
| 15 .54 0.75 2 | 0.468 | 0.356 | 0.467 | 0.419 |
| 15 .54 0.75 3 | 1.000 | 0.382 | 0.694 | 0.202 |
| 30 .37 0.25 1 | 1.000 | 0.000 | 0.593 | 0.317 |
| 30 .37 0.25 2 | 0.480 | 0.342 | 0.629 | 0.315 |
| 30 .37 0.25 3 | 0.768 | 0.296 | 0.760 | 0.185 |
| 30 .37 0.50 1 | 0.980 | 0.020 | 0.906 | 0.159 |
| 30 .37 0.50 2 | 0.510 | 0.434 | 0.583 | 0.342 |

(Continues)
**TABLE 2** continued

| Survey design choices | Population attributes | Model selection | Occupancy estimates |
|-----------------------|-----------------------|-----------------|---------------------|
|                       |                       | Null rejected   | Correct response    | Not underestimated | Within 85% CI |
| Affected sites        | $p^*$                 | $\psi_1$       | Response            |                     |              |
| 30                    | .37                   | .50             | 3                   | 0.998               | 0.450         | 0.802        | 0.131       |
| 30                    | .37                   | .75             | 1                   | 0.988               | 0.012         | 0.710        | 0.339       |
| 30                    | .37                   | .75             | 2                   | 0.474               | 0.400         | 0.551        | 0.359       |
| 30                    | .37                   | .75             | 3                   | 1.000               | 0.398         | 0.703        | 0.199       |
| 30                    | .54                   | .25             | 1                   | 1.000               | 0.000         | 0.556        | 0.287       |
| 30                    | .54                   | .25             | 2                   | 0.578               | 0.412         | 0.591        | 0.356       |
| 30                    | .54                   | .25             | 3                   | 0.702               | 0.198         | 0.825        | 0.162       |
| 30                    | .54                   | .50             | 1                   | 0.926               | 0.074         | 0.731        | 0.174       |
| 30                    | .54                   | .50             | 2                   | 0.520               | 0.710         | 0.339        |              |
| 30                    | .54                   | .75             | 1                   | 0.992               | 0.008         | 0.632        | 0.363       |
| 30                    | .54                   | .75             | 2                   | 0.534               | 0.438         | 0.536        | 0.396       |
| 30                    | .54                   | .75             | 3                   | 1.000               | 0.290         | 0.731        | 0.209       |
| 60                    | .37                   | .25             | 1                   | 1.000               | 0.000         | 0.502        | 0.202       |
| 60                    | .37                   | .25             | 2                   | 0.538               | 0.374         | 0.736        | 0.210       |
| 60                    | .37                   | .25             | 3                   | 0.924               | 0.526         | 0.941        | 0.053       |
| 60                    | .37                   | .50             | 1                   | 0.994               | 0.006         | 0.934        | 0.146       |
| 60                    | .37                   | .50             | 2                   | 0.556               | 0.470         | 0.752        | 0.205       |
| 60                    | .37                   | .50             | 3                   | 1.000               | 0.508         | 0.934        | 0.055       |
| 60                    | .37                   | .75             | 1                   | 0.998               | 0.002         | 0.646        | 0.328       |
| 60                    | .37                   | .75             | 2                   | 0.508               | 0.458         | 0.702        | 0.238       |
| 60                    | .37                   | .75             | 3                   | 1.000               | 0.456         | 0.825        | 0.144       |
| 60                    | .54                   | .25             | 1                   | 1.000               | 0.000         | 0.456        | 0.179       |
| 60                    | .54                   | .25             | 2                   | 0.642               | 0.426         | 0.677        | 0.272       |
| 60                    | .54                   | .25             | 3                   | 0.846               | 0.482         | 0.955        | 0.045       |
| 60                    | .54                   | .50             | 1                   | 0.944               | 0.056         | 0.774        | 0.099       |
| 60                    | .54                   | .50             | 2                   | 0.616               | 0.458         | 0.684        | 0.270       |
| 60                    | .54                   | .50             | 3                   | 1.000               | 0.580         | 0.939        | 0.058       |
| 60                    | .54                   | .75             | 1                   | 0.998               | 0.002         | 0.564        | 0.278       |
| 60                    | .54                   | .75             | 2                   | 0.574               | 0.492         | 0.635        | 0.306       |
| 60                    | .54                   | .75             | 3                   | 1.000               | 0.378         | 0.891        | 0.103       |

**TABLE 3** Amount of variation in statistical power explained by each simulation parameter (pseudo-$R^2$)

| Parameters (Table 1) | Model selection | Occupancy estimates |
|----------------------|-----------------|---------------------|
|                      | Null rejected   | Correct response   | Not underestimated | Within 85% CI |
| Study design choices |                 |                    |                     |              |
| Affected sampling sites | 0.017          | 0.096             | 0.233              | 0.089       |
| Detection probability ($p^*$) | 0.000          | 0.001             | 0.002              | 0.003       |
| Population attributes |                 |                    |                     |              |
| Initial occupancy ($\psi_1$) | 0.015          | 0.039             | 0.019              | 0.007       |
| Response type | 0.515          | 0.704             | 0.363              | 0.607       |
when the two were included in a post hoc bivariate generalized linear model, the two explained 60% of the variation, suggesting that the methodological and ecological aspects of a scenario were accounting for separate and largely additive processes affecting variation in statistical power. Statistical power to not underestimate the effect of a megafire on site occupancy was generally <0.8; power was highest for response 3 but again was generally <0.8 (Figure 1b; Figure 2a; Table 2). The number of affected sites was more important, explaining 23% of the variation in statistical power to not underestimate the effect of a megafire on site occupancy, while response type explained 36% of the variation; together, they explained 60% of the variation (Table 3).

Under most scenarios, monitoring programmes performed slightly worse than chance (<0.5) when choosing between the BACI-static and BACI-ephemeral dynamic occupancy models, and almost never correctly identified ephemeral, positive responses to megafires (i.e., response 1) (Figure 1c; Figure 2c,d). Response type explained most of the variation in statistical power (pseudo-$R^2 = .704$) and was the only aspect of a monitoring scenario that explained >4% of the variation in statistical power (Table 3). Statistical power to accurately estimate occupancy (i.e., the 85% confidence intervals of the top occupancy model overlap true occupancy at burned sites) was uniformly very low (Figure 1d). Statistical power to correctly estimate occupancy was lowest for the species most negatively affected by fire (response 3), but monitoring programmes were best able to correctly identify that population response (Figure 2a). Response type again explained the most variation in statistical power (pseudo-$R^2 = .607$), though the number of affected sites explained 9% of the variation (Table 3).

As noted above, the simulation tutorial is freely available (Supporting information) and explains how each parameter can be changed to suit user’s needs (including creating “after-only” or “impact-only” versions of the BACI design). Thus, if a relevant
scenario is missing from Table 2 (i.e. was not considered in these analyses), it can be created.

3.2 | Sierra Nevada case study results

The results of the Sierra Nevada case study simulations followed the same patterns as the generalized simulations reported above. Statistical power to identify any Spotted Owl response to megafire (via model selection) was 0.62–0.88, with lower detection probability leading to greater power (Table 4). Yet, increased detection probability led to increased statistical power to detect the minimum effect of a megafire on site occupancy (0.86 versus 0.77). Statistical power to identify the correct megafire response (via model selection) or the correct occupancy rates (via estimated occupancy) was low (Figure 3).

Statistical power to identify any Black-backed Woodpecker response to megafire was 1.0 regardless of detection probability, and power to detect the minimum effect of a megafire on site occupancy was 0.70–0.66, with power decreasing with increasing detection probability (Table 4; Figure 3). Similarly, statistical power to estimate site occupancy correctly was greater when detection was lower.
The monitoring programme was unable to identify the correct population response via model selection (i.e. the BACI-ephemeral dynamic occupancy model) (statistical power < 0.08). Importantly, the occupancy and detection estimates reported in the literature were derived using species-specific vocal lure surveys, not passive acoustic surveys, so those values (particularly seasonal detection probability) could differ substantially under a different sampling approach.

4 | DISCUSSION

Biodiversity conservation in the face of the looming, but uncertain threat posed by megafires is complicated by species-specific responses to fire. Species of management concern may not be suitable umbrella species for their entire communities (e.g., Burnett & Roberts, 2015), and sometimes large, severe fires may have opposing implications for focal species (e.g., the Spotted Owl and Black-backed Woodpecker [Jones et al., 2016; Tingley et al., 2018], or the Flame Robin compared to 12 other birds in south-eastern Australia [Lindenmayer et al., 2014]). Implementing holistic ecosystem management plans will require understanding varying and sometimes conflicting trade-offs, both among species and among objectives such as biodiversity conservation and ecosystem restoration (Wood & Jones, 2019).

Forest management is further complicated by the temporal trade-offs managers may face in balancing the short-term costs of fuel reduction treatments to sensitive species against the desired long-term benefits (Wood et al., 2018). In short, understanding species' responses to megafires is a difficult but urgent task. These simulations suggest that in most cases landscape-scale monitoring programmes can provide high statistical power to determine whether wildlife populations have changed in response

**TABLE 4** Statistical power to detect Spotted Owl and Black-backed Woodpecker responses to megafires in the existing Sierra Nevada acoustic monitoring program

| Species                    | Sites | $p^a$ | Initial occupancy | Response | Model selection | Occupancy estimates |
|----------------------------|-------|-------|-------------------|----------|-----------------|---------------------|
|                            |       |       |                   |          | Null rejected   | Correct response    |
|                            |       |       |                   |          | Correct response| Not underestimated |
|                            |       |       |                   |          |                 | Within 85% CI       |
| Spotted Owl                | 4     | .75   | 0.5               | 3        | 0.878           | 0.600               |
|                            |       |       |                   |          | 0.622           | 0.108               |
|                            | 90    |       |                   |          | 0.769           | 0.040               |
| Black-backed Woodpecker    | 12    | .75   | 0.25              | 1        | 0.998           | 0.002               |
|                            |       |       |                   |          | 1.000           | 0.000               |
|                            | 90    |       |                   |          | 0.697           | 0.386               |
|                            |       |       |                   |          | 0.659           | 0.352               |

$^a$ Seasonal detection probability.
to large patches of high-severity fire, an increasingly common attribute of megafires (Stevens et al., 2017), or other spatially extensive and relatively homogeneous disturbance. However, the results are likely to lack nuance: reliably identifying ephemeral responses and accurately estimating site occupancy may not be possible, especially with only five years of post-fire data as considered here (Banner et al., 2019).

The most important population attribute affecting statistical power was the species response to fire: more pronounced responses—positive or negative—to fire were more likely to be identified than a moderate, ephemeral negative response. Landscape-scale monitoring programmes may therefore be unsuitable for rapidly identifying subtle responses to fire, so the absence of evidence for such responses should only with caution be construed as evidence of absence. Identifying changes in local survival is more challenging when local survival varies among sites (Popescu et al., 2012), so control sites should be as ecologically and demographically similar to burn sites as possible—ideally, pre-fire habitat and site extinction/colonization in control and impact sites would be indistinguishable. In these simulations, using four times as many control sites as burned sites balanced swamping the effects of the fire with unaffected sites and having low precision because of small sample size (Popescu et al., 2012).

The number of affected sites was the most important determinant of statistical power from a study design perspective. While researchers cannot determine how much of their study area may burn at high severity (or be subject to some other spatially extensive disturbance), there are at least three ways to influence potential sample size, each of which entails trade-offs between resource availability and desired statistical power and are informed by the probability of a megafire occurring. First, increasing sampling density (e.g., from 15% to 25% of the landscape) will ensure that more area within any given disturbance is surveyed. Second, stratifying sampling to increase survey density in areas that are more likely to experience fire could lead to more affected sites, though this would complicate population trend assessments. Third, implementing a hierarchical design such that co-deployed detectors (e.g., ARUs or camera traps) jointly provide data about some species and yield independent data about others would yield higher sample sizes for the latter group of species. The paradoxical finding that lower seasonal detection probability led to higher power in several cases is likely driven by the fact that lower detection probability leads to lower precision and thus a greater chance of the 85% confidence intervals containing the true occupancy value.

The results of the Sierra Nevada case study suggest that the acoustic monitoring programme in that region will likely be adequate to provide rudimentary information on two prominent fire-affected birds, the Spotted Owl and Black-backed Woodpecker, five years post-fire. Whether a given megafire affected the population of either species is likely to be reliably measured (power to reject the null hypothesis $= 0.622–1.00$), but further details, such as ephemeral responses to post-fire conditions or even accurate site occupancy estimates, may not be attainable. It is therefore unlikely that Sierra Nevada acoustic monitoring programme’s current design will be capable of replicating the type of BACI experiments that a long-term mark-recapture study provided in the aftermath of the 2014 King Fire (Jones et al., 2016). However, landscape-scale studies are not designed to provide detailed fine-scale information. Data from the acoustic monitoring programme can support inferences that even networks of fine-scale mark-recapture studies cannot: landscape-scale insights arising from a randomized design (Wood et al., 2019).

The biggest strength of landscape-scale monitoring projects may lie not in their ability to detect the effects of one fire, but to measure the effects of many fires. If multiple megafires occur in a single season, affected monitoring sites from multiple fires could be pooled (within reasonable context-dependent limitations) to effectively increase sample size and move beyond a single-fire focus. Alternatively, comparing site occupancy to fire history for all sites in a monitoring programme could allow researchers to infer colonization rates based on the duration of post-fire vacancy, which, in turn, could be used to develop mechanistic understandings of focal species and even whole communities’ responses to megafires (Wood et al., 2021). The proliferation of landscape-scale monitoring programmes, especially in the western United States, represents a further opportunity to increase sample sizes: if acoustic, camera or other data from multiple monitoring programmes can be pooled and analysed in a unified framework, regional-scale understandings of species’ responses to fire and other disturbances may be attainable (Rich et al., 2019). Moreover, such an approach would be better able to reflect the nuanced responses to fire that many species exhibit—and which are minimized in simulations such as these. For example, pyrodiversity supports age-dependent Black-backed Woodpecker foraging (Stillman et al., 2019) and influences Spotted Owl foraging habitat selection (Jones et al., 2020), and increasing sample size by including many burned sites could support the inclusion of variables such as distance to unburned habitat and patch shape complexity.

Large patches of high-severity fire, as considered in these simulations, may result in substantial displacement of individuals of large-bodied and/or volant species, rather than outright mortality. A possible outcome of such movements, either by resident or migratory species, is increased population density adjacent to the fire. Acoustic surveys of small-bodied species may be capable of detecting these changes because the vocal activity rate—as opposed to detection/nondetection data, as considered in this simulation—can be used to estimate population density (Pérez-Granados et al., 2019). Within-site changes would be difficult to measure for territorial species whose home ranges are larger than the detection radius of the survey device, but visual or acoustic differentiation of individuals could facilitate such analyses (Wood et al., 2020).

In the context of identifying the effects of individual megafires, small-bodied species with relatively limited spatial requirements may be the optimal umbrella species, a reversal of conventional approaches in which large-bodied species are often treated as umbrella species because of their relatively vast spatial requirements.
For example, Hermit Warblers (Setophaga occidentalis) are strongly associated with Spotted Owl habitat in the Sierra Nevada (Burnnett & Roberts, 2015) but are just ~2% the weight of Spotted Owls and are therefore likely to maintain much smaller territories (Haskell et al., 2002). Under the hierarchical design used in the existing Sierra Nevada acoustic monitoring programme, co-deployed ARUs 500–1660 m apart constituting a single Spotted Owl survey site could serve as independent Hermit Warbler sites (putatively independent point counts are as close as 250 m). This instantly doubles or triples the number of affected survey sites, thus increasing statistical power. To the extent that similar habitat requirements lead to similar responses to disturbance, the responses of smaller-bodied species to large, severe fires and other spatially extensive disturbances could be statistically powerful proxies for the lower-power estimates of larger-bodied species’ responses. Of course, the validity of linking habitat associations and disturbance responses would need to be examined carefully.

Charismatic species with existing or potential legal protection are likely to continue to impel funding for landscape-scale monitoring efforts. Although prominent species such as the Spotted Owl may not represent the diverse ecological needs of entire communities (Burnnett & Roberts, 2015; Latif et al., 2016; Lindenmayer et al., 2014), the monitoring programmes those species justify yield community-level data (Rodhouse et al., 2019; Wood et al., 2014), the monitoring programmes those species justify demonstrate that passive acoustic monitoring and other non-invasive sampling techniques can support research on multiple species’ populations a unified framework. By helping to justify such programmes, charismatic habitat specialists such as the Spotted Owl may indirectly provide ecosystem-wide conservation benefits and thus provide a far broader protective umbrella than ever before.

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SUPPORTING INFORMATION
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