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Effects of interactions between anthropogenic stressors and recurring perturbations on ecosystem resilience and collapse

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Abstract

Insights into declines in ecosystem resilience and their causes and effects can inform preemptive action to avoid ecosystem collapse and loss of biodiversity, ecosystem services, and human well-being. Empirical studies of ecosystem collapse are rare and hampered by ecosystem complexity, nonlinear and lagged responses, and interactions across scales. We investigated how an anthropogenic stressor could diminish ecosystem resilience to a recurring perturbation by altering a critical ecosystem driver. We studied groundwater-dependent, peat-accumulating, fire-prone wetlands known as upland swamps in southeastern Australia. We hypothesized that underground mining (stressor) reduces resilience of these wetlands to landscape fires (perturbation) by diminishing groundwater, a key ecosystem driver. We monitored soil moisture as an indicator of ecosystem resilience during and after underground mining. After landscape fire, we compared responses of multiple state variables representing ecosystem structure, composition, and function in swamps within the mining footprint with unmined reference swamps. Soil moisture declined without recovery in swamps with mine subsidence (i.e., undermined), but was maintained in reference swamps over 8 years (effect size 1.8). Relative to burned reference swamps, burned undermined swamps showed greater loss of peat via substrate combustion; reduced cover, height, and biomass of regenerating vegetation; reduced postfire plant species richness and abundance; altered plant species composition; increased mortality rates of woody plants; reduced postfire seedling recruitment; and extirpation of a hydrophilic animal. Undermined swamps therefore showed strong symptoms of postfire ecosystem collapse, whereas reference swamps regenerated vigorously. We found that an anthropogenic stressor diminished the resilience of an ecosystem to recurring perturbations, predisposing it to collapse. Avoidance of ecosystem collapse hinges on early diagnosis of mechanisms and preventative risk reduction. It may be possible to delay or ameliorate symptoms of collapse or to restore resilience, but the latter appears unlikely in our study system due to fundamental alteration of a critical ecosystem driver.

Efectos de las interacciones entre los estresantes antropogénicos y las perturbaciones recurrentes sobre la resiliencia y el colapso de los ecosistemas

KEYWORDS
ecosystem collapse, fire, groundwater hydrology, Newnes Plateau Shrub Swamp, peatland, red list of ecosystems, regime shift, underground mining

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Resumen
La comprensión de la declinación en la resiliencia de los ecosistemas y sus causas y efectos puede orientar las acciones preventivas para evitar el colapso ecosistémico y la pérdida de biodiversidad, servicios ambientales y bienestar humano. Los estudios empíricos del colapso ecosistémico son escasos y se enfrentan a obstáculos como la complejidad del ecosistema, respuestas rezagadas y no lineales e interacciones entre las escalas. Investigamos cómo un estresante antropogénico podría reducir la resiliencia del ecosistema a una perturbación recurrente mediante la alteración de un causante importante. Estudiamos los humedales dependientes de aguas subterráneas que acumulan turbas y son propicios a incendios conocidos como pantanos de tierras altas en el sureste de Australia. Nuestra hipótesis fue que la minería subterránea (estresante) reduce la resiliencia de estos humedales a incendios (perturbación) al disminuir el agua subterránea, un causante clave para el ecosistema. Monitoreamos la humedad del suelo como un indicador de la resiliencia del ecosistema durante y después de la minería subterránea. Después de los incendios, comparamos la respuesta de múltiples variables de estado que representaban la estructura, composición y función del ecosistema en los pantanos dentro de la huella minera con los pantanos referenciales sin minería. La humedad del suelo declinó sin recuperación en los pantanos con hundimientos mineros (es decir, socavones) pero se mantuvo en los pantanos referenciales durante ocho años (tamaño del efecto: 1.8). En relación a los pantanos referenciales incendiados, los pantanos con socavones e incendios mostraron una mayor pérdida de turba mediante la combustión del sustrato; reducción en la cobertura, altura y regeneración de biomasa de la vegetación; reducción en la riqueza y abundancia de especies vegetales post incendio; alteraciones en la composición de especies vegetales; incremento en la mortalidad de las plantas leñosas; reducción en el reclutamiento post incendio de plántulas; y la extirpación de un animal hidrofílico. Por lo tanto, los pantanos con socavones mostraron síntomas fuertes de un colapso ecosistémico post incendio, mientras que los pantanos referenciales se regeneraron vigorosamente. Descubrimos que los estresantes antropogénicos redujeron la resiliencia de un ecosistema a perturbaciones recurrentes, lo que lo predispone al colapso. La eliminación de este colapso depende de un diagnóstico temprano de mecanismos y reducción del riesgo preventivo. Puede ser posible retardar o mitigar los síntomas del colapso o restaurar la resiliencia, aunque lo último parece ser improbable en nuestro sistema de estudio debido a la alteración fundamental de un causante importante del ecosistema.

PALABRAS CLAVE
cambio de régimen, colapso ecosistémico, hidrología de aguas subterráneas, lista roja de ecosistemas, minería subterránea, pantano arbustivo de la meseta Newnes, turbera

人为压力和反复扰动之间的相互作用对生态系统恢复力及崩溃的影响

【摘要】深入了解生态系统恢复力下降的情况及其原因和影响, 可以为避免生态系统崩溃、生物多样性丧失、生态系统服务丧失及人类福祉减少的抢先行动提供指导。然而, 对生态系统崩溃的实证研究非常少见, 并且受到生态系统复杂性、非线性和滞后响应以及跨尺度互作的阻碍。本研究分析了一种人为压力源如何通过改变一个关键的生态系统驱动因素, 来降低生态系统面对反复扰动的恢复力。本研究关注澳大利亚东南部一种依赖地下水、积累泥炭, 且易受火灾影响的湿地类型, 即高地沼泽。我们假设地下采矿(压力源)通过减少地下水这一关键的生态系统驱动因素, 降低了这些湿地对景观火灾(扰动)的恢复力。我们监测了土壤湿度, 以作为地下采矿期间和之后的生态系统恢复力指标。在发生景观火灾后, 我们比较了代表采矿范围内的沼泽地与未采矿的参考沼泽地中生态系统结构、组成和功能的多状态变量的响应情况。研究发现, 在有矿井塌陷(即被破坏)的沼泽地中, 土壤湿度下降且没有恢复, 但在参考沼泽地中, 土壤湿度却可以保持8年(效应量为1.8)。相比于参考沼泽地, 采矿的沼泽地在火灾后出现更多基质燃烧导致的泥炭减少;再生植被的覆盖度、高度和生物量减少;火灾后植物物种丰富度和丰度降低;植物物种组成改变;木本植物死亡率增加;火灾后幼苗补充减

少;还有一种亲水动物发生灭绝。因此,采矿的沼泽地明显表现出火灾后生态系统崩溃的症状,而参考沼泽地则可以旺盛地再生。我们发现,采矿这种人为压力削弱了生态系统对反复扰动的恢复力,使其容易崩溃。避免生态系统崩溃依赖于对机制的早期诊断和预防性的风险控制。推迟或减轻生态系统崩溃的症状或恢复生态系统恢复力也许可行,但在我们的研究系统中,由于一个关键的生态系统驱动因素的根本改变,后者似乎不太可能实现。【**翻译: 胡怡思; 审校: 聂永刚**】

关键词: 生态系统崩溃, 稳态转变, 泥炭地, 纽恩高原灌木沼泽, 火灾, 地下采矿, 地下水水文学, 生态系统红色名录

INTRODUCTION

Ecosystem collapse signals an organizational change in ecosystem properties, including substantial and lasting loss or displacement of biota and reorganization of structure and ecological processes (Bland, et al., 2018; Cumming & Peterson, 2017; Keith, et al., 2013). The mechanisms that drive such transformations are diverse, varying from deterministic forcing to positive feedbacks (Cumming & Peterson, 2017; Dakos et al., 2015), as are the temporal patterns of change that vary from smooth to abrupt (Bergstrom, et al., 2021). Examples include the drying of the Aral Sea and its replacement by hypersaline lakes and ephemeral grasslands (Micklin & Aladin, 2008); regime shifts between clear and turbid states in shallow lakes (Carpenter, 2003); displacement of tropical forests by pasture and plantation systems (Hansen, et al., 2013); desertification of grassy rangelands (Bestelmeyer et al., 2013); and collapse of numerous pelagic marine fisheries and benthic ecosystems (de Young, et al., 2008). Regime shifts are a specific group of mechanisms among the diverse expressions of ecosystem collapse (Keith, et al., 2013); their hallmarks include incremental environmental change, positive feedback mechanisms, hysteresis, and sudden transitions into alternative states that are difficult to reverse (Scheffer et al., 2001).

The structural, compositional, and functional changes associated with ecosystem collapse have important implications for conserving biodiversity and maintaining ecosystem services, the dual global imperatives mandated under the United Nations Convention on Biological Diversity and Sustainable Development Goals (United Nations, 1992, 2015). The consequences of ecosystem collapse for human well-being extend across all sectors from health to economic prosperity (Díaz, et al., 2019).

An understanding of the pathways and mechanisms of ecosystem collapse and how they might be mitigated is imperative to successful conservation strategies and actions, yet these mechanisms are generally complex and poorly understood (Keith et al., 2015; Peterson et al., 2003). Cumming and Peterson (2017) note that "Mechanistic theories of collapse that unite structure and process can make fundamental contributions to solving global environmental problems." Recent work has aimed to detect declines in ecosystem resilience (the capacity to undergo disturbance, persist, and maintain function) as a causal agent and precursor to collapse. Methods for early warning of ecosystem collapse have developed from theory and simple models or natural archives that produce dense time series (Scheffer et al., 2009; Thomas, 2016). Potential early warning signals include critical slowing during recovery from perturbations; increasing asymmetry of fluctuations; "flickering" or stochastic forcing between stable states; and increased coherence among spatial units (Scheffer et al., 2009).

These time-series indicators stem from declines in resilience that, if diagnosed and detected, provide an early warning to design and implement adaptive strategies for risk reduction. We investigated how an anthropogenic stressor (underground mining), acting through a critical ecosystem driver (hydrological regime), could diminish the resilience of an ecosystem to a recurring perturbation (fire), predisposing the ecosystem to elevated risks of collapse (Figure 1). Conversely, we hypothesized that the ecosystem is more likely to recover from perturbations if its resilience is not first diminished by the stressor.

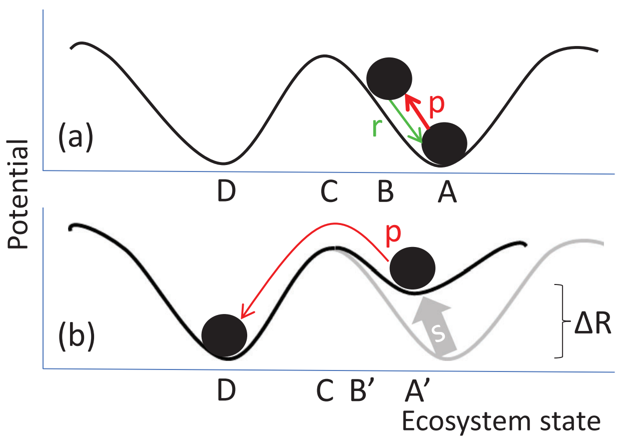

FIGURE 1 Postulated responses of ecosystem resilience (*R*) and ecosystem collapse under scenarios of stress and perturbation: (a) perturbation (*P*) results in a transient shift from state A to B without reaching a tipping point (C), and the system returns to state A through autogenic recovery (*r*) and (b) a stressor (*S*) diminishes resilience of the system through the change in *R* (Δ*R*) and in so doing shifts the system from state A to A′ and, after perturbation, beyond tipping point C to collapsed state D (*y*-axis, potential for spontaneous change; *x*-axis, ecosystem state variable; curves, stable domains and ecosystem resilience and degree of perturbation required to shift the system between alternative stable domains [or difference in potential between local maxima and minima]). In our test case, underground mining (*S*) transforms wetlands from high-resilience ecosystems (scenario in [a]) to low-resilience ecosystems, with fire (*P*) triggering collapse (scenario [b]), rather than autogenic recovery to the initial state.

Case studies and pathologies have been instrumental to developing theory on ecosystem resilience and collapse (Bergstrom et al., 2021; Cumming & Peterson, 2017; Holling, 1973; Scheffer et al., 2001), as have mathematical models derived from systems resilience theory (Dakos et al., 2015; Scheffer et al., 2009). Yet, robust empirical studies examining the mechanisms of ecosystem resilience and collapse are extremely rare (Scheffer et al., 2001). The difficulties of investigation relate to ecosystem complexity, unpredictability, and nonlinearity of change, ecological lags in responses, large organizational scales, and interactions across scales, as well as logistic challenges of replication and definition of suitable experimental controls or reference systems.

Our study system is a type of groundwater-dependent, peat-accumulating wetland ecosystem (known locally as upland swamps) in a landscape with a long history of recurring landscape fires (a perturbation regime). We hypothesized that hydrological change caused by underground mining (an anthropogenic stressor) diminishes the resilience of these wetlands to fires. We first described the postulated mechanism of collapse and then examined empirical evidence that underground mining initiates changes in groundwater hydrology, a key driver of the wetland ecosystem. We then measured a wide range of state variables as the ecosystem regenerated after fire to examine differences in response between wetlands exposed to underground mining relative to reference systems located beyond the mining footprint. We reviewed the consequences and irreversibility of collapse of these ecosystems and identified management strategies for impact avoidance. Finally, we considered the broader ecosystem management implications for early detection and risk-reduction strategies, given ecological lags between the initiation of the stressor and the transition to collapse.

METHODS

Study system

Our study ecosystem was a group of geographically restricted peat-accumulating, groundwater-dependent palustrine wetlands (hereafter upland swamps) in the upper Blue Mountains in the Sydney stratigraphic basin (centered on latitude 33°23′ S, longitude 150°13′ E), southeastern Australia (Appendix S1). These peaty wetlands are listed as endangered ecological communities under national legislation as "Temperate Highland Peat Swamps on Sandstone" (DEWHA, 2005) and in New South Wales as "Newnes Plateau Shrub Swamps" (NSW Scientific Committee, 2005). They are treeless ecosystems within a eucalypt forest matrix characterized by dense growth of hydrophilic sclerophyll shrubs and graminoids, with many hydrophilic specialists and some local endemics represented in the flora and fauna (Benson & Baird, 2012). High levels of subsoil moisture are sustained by perched aquifers on friable sandstones of the Triassic Narrabeen Group interbedded with low-permeability claystone strata (Benson & Baird, 2012). Basal dates of sediments suggest the peatlands developed during the Pleistocene–Holocene transition when the climate became warmer and wetter (Black et al., 2008; Chalson & Martin, 2009; Young, 2017). Charcoal throughout the peaty sediments indicates a long history of fire (Chalson & Martin, 2009), although fire activity varied, declining from the Pleistocene–Holocene transition and increasing again from the mid-Holocene (Black et al., 2008).

Sediments and vegetation function as landscape sponges that retain, filter, and slowly release high-quality water, even during prolonged dry periods (Cowley et al., 2018). These landscape hydrological functions are linchpins of ecosystem services to Sydney's largest city and surrounding regions, including provision of potable water, recreational resources, carbon sequestration, and flood mitigation (e.g., Cowley & Fryirs, 2020). Coal is extracted from the Lithgow Coal Seam 200–400 m below the surface of the Newnes Plateau. Mining leases currently cover about two thirds of the swamp distribution totaling 650 ha (Krogh et al., 2022), and extraction is complete or underway in a substantial portion of that area (Appendix S1). Underground mining, particularly longwall mining methods, causes cracking and collapse of overlying bedrock into the void after seam extraction and associated subsidence of the land surface. This can affect swamp hydrology by depressurizing aquifers, increasing bedrock permeability, triggering movement and fissuring along preexisting geological joints, and warping of the surface, which is accompanied by changes in surface flow (Krogh et al., 2022; Mason et al., 2021; Young, 2017). Once a swamp is affected, groundwater levels usually fall below bedrock with significant desiccation of peat and reduced soil moisture (e.g., Mason et al., 2021).

Model of ecosystem resilience and collapse

Three environmental conditions are critical to formation and persistence of upland swamps (Keith et al., 2014; Young, 2017): a humid climate (precipitation exceeding evapotranspiration), low topographic relief (slow runoff rates), and perched aquifers (low substrate permeability).

Fires consume standing vegetation, liberate resources, stimulate regenerative processes, and may locally consume peaty substrates depending on their prefire moisture content (Prior et al., 2020). Functional upland swamps have a resilient response to fire (Figure 2), returning to prefire "basin of attraction" through autogenic processes (Folke et al., 2004). Resilience of the system rests on positive feedbacks in which abundant subsoil moisture limits combustion of peat; promotes dense vegetation that traps sediment, which interrupts water flow; and maintains a moist, shady microclimate, limiting entry of nonhydrophiles into the system (Young, 2017). Rapid postfire regrowth enables upland swamps to function as refuges for fauna and hydrophilic flora in the burned landscape amid the more slowly regenerating forest matrix.

We hypothesized ecosystem collapse when extreme drying of the peaty substrate diminishes resilience of the system to fire. Ecosystem collapse may occur locally, in a single swamp, or globally when all swamps transition (Keith et al., 2013).

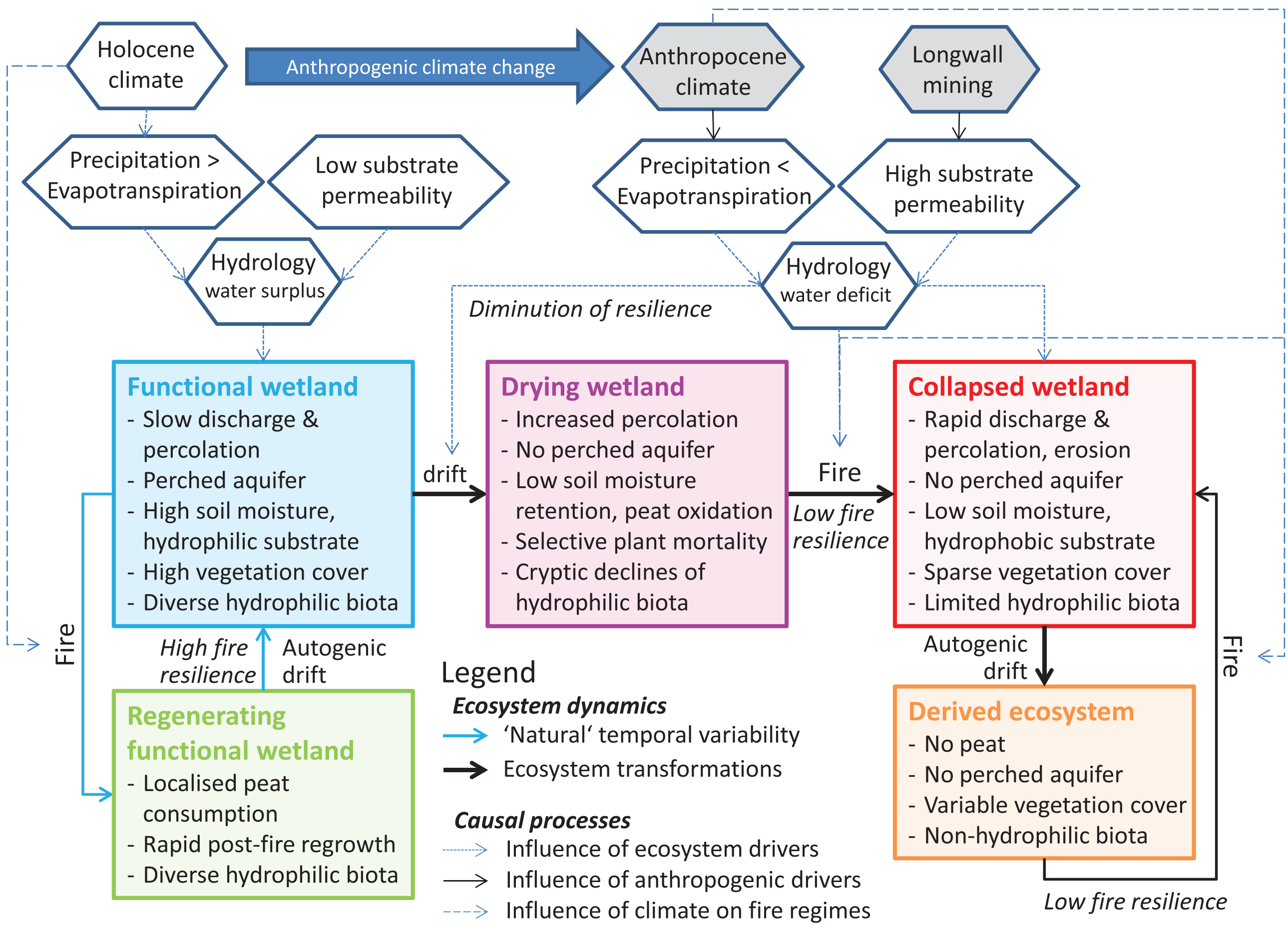

FIGURE 2 Conceptual model of ecosystem dynamics for groundwater-dependent, peat-accumulating wetlands (upland swamps) in 3 states: functional (maintained by positive vegetation–soil–moisture feedbacks), drying (due to, e.g., longwall mining [short timescales] or climate change [long timescales]; lessened fire resilience), and collapsed (triggered by fire after drying).

The initial transition from a functional to a drying wetland state (Figure 2) may be cryptic due to lagged persistence of dense vegetation as hydrological function declines, albeit with selective deaths of hydrophilic plant species. Persistence of dense vegetation, even when branches and shoots have partially senesced, maintains some moisture in the microclimate and limits entry of nonhydrophilic biota. We hypothesized that, due to reduced retention of substrate moisture (Mason et al., 2021), a drying state is predisposed to severe consumption of peat and surface vegetation during fires. This results in transition to a collapsed state with further loss of hydrological function, mortality of standing hydrophilic plants and seedbanks, and consequent failure of regenerative processes that typify resilient and functional swamps (Figure 2).

Longwall mining is the primary anthropogenic driver of wetland drying and collapse (Figure 2). It involves complete extraction of a deep underground coal seam, allowing overburden rock to fall into the void, with associated upward shattering and cracking of bedrock and warping, subsidence, upsidence, and cracking at the surface (Booth, 2006; Krogh, 2007). This alters hydrology by increasing the permeability of the substrate beneath the peatlands and by altering surface flows. We hypothesized that climate change is a secondary anthropogenic driver of wetland drying (Figure 2) that alters hydrology over long timescales by increasing evapotranspiration relative to precipitation (Keith et al., 2010, 2014), subject to large interannual variability and regional climate cycles, with complex biochemical processes governing the breakdown of peat (Davidson & Janssens, 2006; Limpens et al., 2008).

Experimental design and data collection

To determine whether mining-induced changes in hydrology weakened ecosystem resilience to fire, we compared the postfire responses of wetlands that had underground mining beneath them during 2013–2017 (Krogh et al., 2022) with those of unmined reference wetlands (i.e., the 2 transitions labeled *Fire* in Figure 2). We tracked changes in resilience by monitoring soil moisture content. We predicted that contrasting postfire responses of ecosystem resilience and collapse would be detectable through differences between reference peatlands and those influenced by longwall mining in peat retention and consumption; postfire vegetation structure and biomass; plant species richness and composition; plant population processes (survival and reproduction); and hydrophilic fauna.

We contextualized changes in ecosystem resilience by monitoring soil moisture annually from 2015 to 2022 during summer in 3 swamps affected by mine subsidence and 3 unmined reference swamps (Appendices S1 & S2). Measurements were taken at least 24 h after rainfall in January or February each year, except in the summer of 2019–2020 (taken in December toward the end of an extended drought and just prior to the bushfire) and the summer of 2021–2022 (taken in early March after extended rainfall). During each annual monitoring event, we measured volumetric soil moisture content with an MP406 Soil Moisture Sensor Instant Reading Kit with a 6-cm probe (ICT International, Armidale), which uses a standing wave oscillator to generate an electrical field to detect dielectric properties related to moisture content of a substrate. We measured soil moisture in 10 replicate circular plots (1-m radius) on the valley floor and sides within each swamp based on the mean of 3 randomly placed insertions of the probe.

To examine ecosystem responses to fire, we sampled vegetation and soil variables in 5 swamps affected by mine subsidence and 5 reference swamps, including the 6 sampled for soil moisture and a hydrophilic reptile species (Appendices S1 & S2). There were no other substantive pressures that differed between undermined and reference swamps other than mining treatment. All sites were within a 10 × 5 km area and elevational range of 990–1120 m above sea level and hence were climatically similar (Appendix S3). All sites were burned on 16 December 2019 during extensive east Australian bushfires. Four of the sites (2 undermined and 2 reference) were also burned in October 2013, 1 reference site was burned in January 2003, and the remaining 5 sites had been unburned since prior to 1980 (Appendix S2).

In each swamp, we established separate 20- m transects parallel to the swamp drainage line on the valley floor and the valley side to encompass variation in vegetation and hydrology. Transects were sampled during 4–6 March 2020, approximately 10 weeks after fire, except sites CC and EW, which were sampled on 24 August 2020 (Appendix S4). Site BUD was only sampled in a second survey (see below). We measured 3 metrics of fire severity (Keeley, 2009) on the transect: scorch height (representing flame height), the lowest unscorched prefire plant tissues remaining; proportion of prefire foliage consumed or scorched for the woody and nonwoody components of the vegetation, respectively; and mean diameter of the smallest remaining twig or branch ($n = 10$) (Whight & Bradstock, 1999).

To quantify vegetation structure, we measured the height (upper and lower bounds and mode) and visually estimated projective cover of live shrubs and graminoids in each transect. We also collected samples of aboveground live biomass (postfire regrowth) from four 0.5 × 0.5 m quadrats spaced at 5-m intervals along a line located parallel to, and 5 m from, each transect in similar vegetation to that along the transect. Samples were stored in clean paper bags, dried in an oven at 60°C until mass was stable, and weighed in the laboratory.

We assessed peat loss during the fire by first visually estimating the percentage of the surface affected by peat consumption within the 20 × 1 m area of each transect and then measuring the maximum vertical distance from the current soil surface to the prefire soil level inferred from morphology and markings of exposed and charred root stocks of woody plants. We calculated an index of peat consumption from the product of these 2 values.

We identified and counted vegetatively resprouting individuals (V), dead remains of woody plants (D) (i.e., individuals with no regenerating tissues), and seedling recruits of all vascular plant taxa within each contiguous 1 × 1 m quadrat along the 20-m transects. Reconnaissance after survey in March 2020 indicated that some plants had delayed postfire resprouting or germination responses (e.g., physiologically dormant species). We therefore resurveyed all plots in November 2020 to ensure that the species composition of regenerating vegetation was fully sampled across the first postfire year. One reference site (BUD) was sampled only in the November survey. For all taxa, we estimated survival rates ($V/[V + D]$) and the maximum density of seedling recruitment across the March and November surveys.

To examine the response of ecosystem fauna, we monitored abundance of a locally endemic lizard, *Eulamprus leuraensis* (Blue Mountains water skink), an endangered species with a narrow hydrophilic environmental niche restricted to upland swamps. Skinks were trapped annually from 2015 to 2022 at the same 6 sites as those monitored for soil moisture (Appendix S1). At each site, each year on a day with a maximum temperature 20–35°C and no rainfall, we set 9 unbaited funnel traps and 1 pitfall trap approximately 10 m apart, except in 2022 when 10 funnel traps were deployed (Gorissen et al., 2017).

Data are available at Open Science Framework (https://osf.io/ak2w3/).

Data analyses

We fitted a mixed log-linear model to examine temporal trends in soil moisture in relation to mining treatment and rainfall during the 3 months prior to soil measurement (rainfall data for November–January from Bureau of Meteorology, Lithgow [Cooewull] station 63226, 33.48° S, 150.13° E, 900 m elevation, approximately 12 km west of the study area) (Appendix S3). The model included an interaction term between mining influence (factor with 2 levels) and log-transformed time ($t + 1$) in years (continuous), a main effects term for rainfall (continuous), and a random factor for site.

We used linear models to test the effects of underground mining and landform on fire severity (twig diameter), peat consumption, vegetation structure (height and cover of woody and nonwoody plant strata, respectively), soil chemistry, plant biomass, plant survival and recruitment, and species richness (woody and nonwoody). The models had 2 fixed factors (mining and landform) and an interaction term, with transects as replicates ($n = 20$). Each of the factors had 2 levels (mining influence: yes or no; landform: valley floor or valley side). Models for all variables except plant survival and reproduction were fitted with normal error distributions and identity link functions. The data were log transformed to improve residuals where assumptions for mean variance, homoscedasticity, and normality did not hold.

We compared species composition between longwall-mined and unmined reference swamps and landform types with a 2-factor multispecies generalized linear model of abundances (combined counts of resprouts and postfire recruits) in the R package mvabund (Wang et al., 2012). To accommodate variation in the timing of species responses through the first postfire year, we took the maximum estimated abundance (combined counts of resprouts and seedlings) of that recorded in the March and November surveys for each species in each transect. Of 134 plant taxa recorded in either survey, we included 43 species in the multivariate model based on their occurrence in at least 4 (20%) of the 20 transects. We fitted the models with a negative binomial distribution with log link and checked residuals to confirm satisfactory representation of mean–variance relationships in the data. We removed terms with weak effects to simplify the multispecies model and carried out univariate tests to identify species that had the strongest responses to the remaining factors. The p values were adjusted to control the family-wise error rate across species with a resampling-based implementation of Holm's step-down multiple testing procedure (Wang et al., 2012).

To visualize compositional relationships among samples, we constructed a global nonmetric multidimensional scaling (GNMDS) ordination in 2 dimensions based on pairwise Bray–Curtis dissimilarity values in the R package vegan (Okansen et al., 2020). An Epsilon threshold was set at 0.95 to convert higher Bray–Curtis values to geodesic distances. Optimum (lowest stress) configurations were selected from 100 runs derived from random initial configurations with a maximum of 200 iterations for convergence to achieve convergence ratio 0.99999 from successive stress values. The 2 ordinations with the lowest stress values were compared with a Procrustes test and were identical ($r = 1$, $p = 0.001$, permutations = 999).

For woody plant species with regenerative organs, we estimated plant survival as the proportion of individuals of species that had new foliage by the November 2020 survey ($V/[V + D]$, see previous section). Transects ($n = 20$) were replicates for each species. The proportion of survivors was analyzed using linear mixed models with the same factorial design as above, but with species added as a random independent variable and a binomial error distribution with logit link function to accommodate the bounded proportional values. Density of postfire seedling recruits was analyzed with the same model; a 1-factor multispecies generalized linear model of abundances was used to test effects of mining treatment.

We used a linear model with a Poisson error to compare trends in skink abundance by testing an interaction between mining treatment and time with the summer rainfall tally as a covariable (see soil moisture model). All linear models were constructed in the R package lme4 (R Core Team, 2020).

RESULTS

Ecosystem drivers

Soil moisture levels declined in undermined swamps, whereas they were maintained in unmined reference swamps (mining:time interaction $t = 13.42$, $p << 0.00001$) (Figure 3). Declines in soil moisture began to occur soon after coal extraction and all 3 undermined swamps fell below 50% soil moisture by 2018 (Figure 3). After the 2019 fire, soil moisture rarely exceeded 30% in undermined swamps, whereas soil moisture remained in the range of 70–95% in unmined reference swamps throughout 2014–2015 to 2021–2022. Although prior rainfall had a positive effect on soil moisture ($t = 5.55$, $p < 0.00001$), and the trend varied among individual swamps (variance component 9.25, 95% confidence interval [CI]: 4.52–18.95), differences between undermined and reference swamps were maintained through dry and wet years (92 mm in summer 2019–2020, 560 mm in summer 2021–2022) and appeared to be irreversible.

Scorch height and percent foliage consumed or scorched were uninformative indicators of fire severity because all foliage in all 20 transects was completely consumed and scorch height always reached the highest branches of the tallest plants. Twig diameter data also showed no evidence of differences in fire severity among mining treatments (interaction and main effects $t < 1.72$, $p > 0.2$) (Figure 4a).

Ecosystem state variables

Mining treatment had a strong effect on peat loss ($t = 3.96$, $p = 0.0019$) (Figure 4b); the peat consumption index was more than 5-fold greater in undermined swamps compared with unmined reference swamps. The main effects term for landform types and its interaction with mining had no effect on peat loss ($p = 0.87$ and $p = 0.34$, respectively).

The cover of shrubs 10 weeks postfire in undermined swamps was >95% less than their cover in unmined reference swamps ($t = 5.81$, $p < 0.0001$) (Figure 4c), and cover of nonwoody ground layer was 20% less ($t = 5.21$, $p = 0.0002$) (Figure 4f), a difference that was sustained through the first postfire year (Appendix S5). Height of regenerating shrubs in undermined swamps was 50% less than that in reference swamps ($t = 3.23$, $p = 0.0072$) (Figure 4d). Although shrub cover and height increased over time, the difference in shrub height increased during the first postfire year and the difference in cover was maintained (Appendix S5). There was initially weak evidence of reduced height of regenerating nonwoody vegetation in undermined swamps ($t = 2.00$, $p = 0.063$) (Figure 4e), but within a year after fire, stronger differences were evident between undermined and reference swamps ($t = 3.18$, $p = 0.0051$) (Appendix S5). There was no effect of landform on any measured features of vegetation structure (Figure 4c–f).

Biomass production of regenerating vegetation inundermined swamps was 98% less than that in unmined reference swamps during the first 10 weeks after fire ($t = 7.06$,

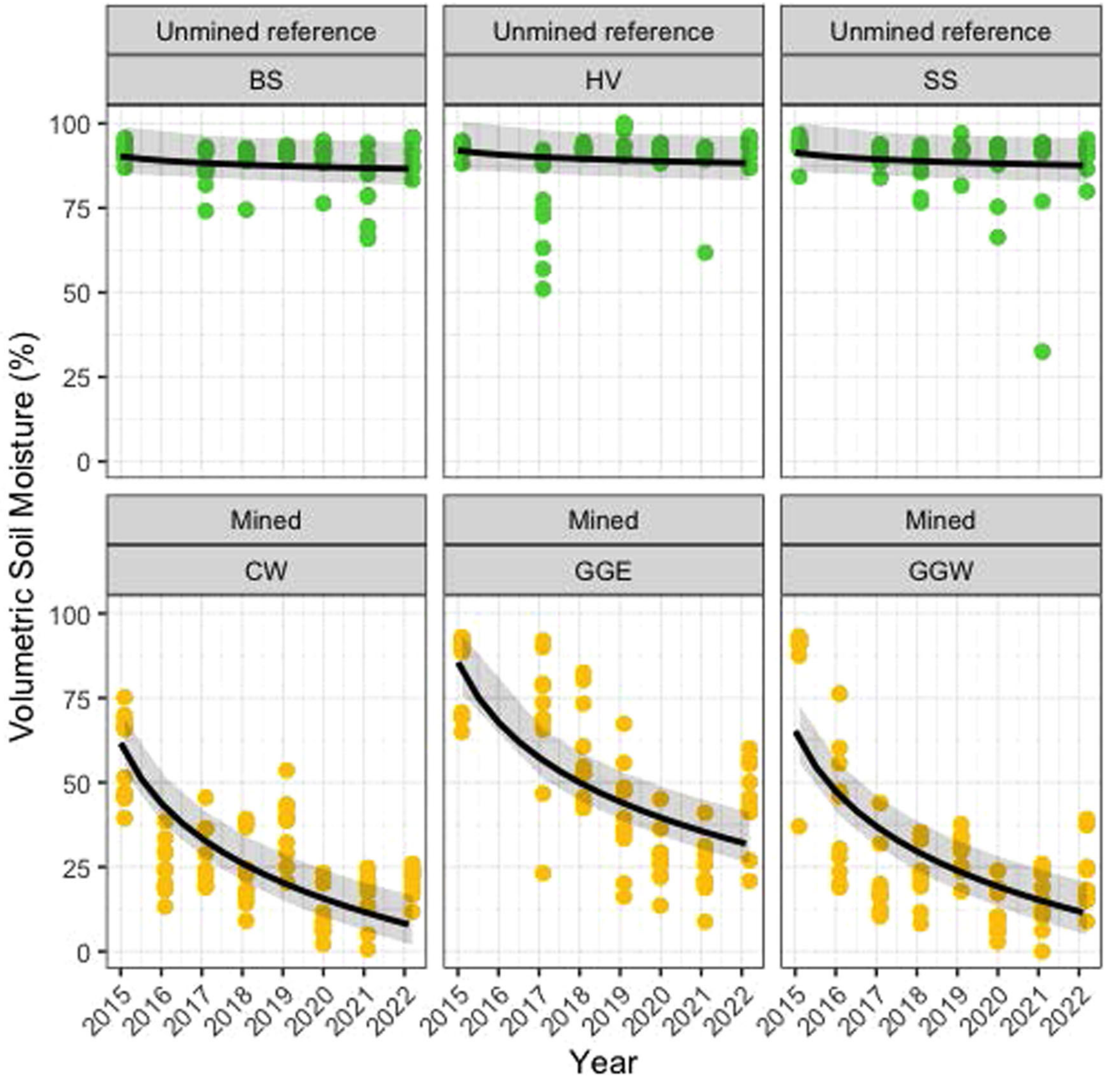

FIGURE 3 Trends in soil moisture indicative of ecosystem resilience in 3 unmined reference swamps (top) and 3 swamps exposed to underground longwall extraction of coal during 2014–2017. Fitted lines are log-linear models soil moisture ~ mining treatment × log (time) + rainfall. The 95% confidence intervals were estimated using a nonparametric case bootstrap coupled with individual residual bootstrap for the range of rain values across all years. Unmined reference sites are Broad swamp (BS), Happy Valley (HV), and Sunnyside (SS); undermined treatment sites are Carne West (CW), Gang Gang East (GGE), and Gang Gang West (GGW) (see Appendix S1).

$p = 0.00001$; Figure 4g). Substantial regrowth occurred over the ensuing months, but differences were maintained. Biomass was still 89% less in undermined swamps than reference swamps 11 months after fire (Appendix S5). Biomass of postfire regrowth was unaffected by landform ($p > 0.5$).

Plant species richness of postfire regrowth was 33% less in undermined swamps relative to unmined reference swamps ($t = 2.92$, $p = 0.013$) (Figure 4h), a pattern that was maintained 11 months after the fire, despite increases in richness across all treatments due to delayed germination of some species (Appendix S5). Richness was unaffected by landform irrespective of time since fire (main effects and interaction $p > 0.7$ after 10 weeks, $p > 0.15$ after 11 months).

A strong effect of longwall mining on plant species composition within the regenerating swamps was evident 10 weeks after fire. Samples from unmined reference sites clustered together in the ordination (stress = 0.091), and undermined sites dispersed more widely and strongly separated from the reference sites (Figure 5). The greater dispersion of undermined samples is likely due to their lower richness and abundance of species. Landform had a secondary influence on species composition; valley floor sites had more positive scores than corresponding valley side samples on the first ordination axis (Figure 5).

Species abundances differed between undermined and unmined reference swamps (Wald = 13.3, $p = 0.016$). Of 43 plant species with sufficient occurrence for analysis, 5 species were recorded exclusively in unmined reference swamps and 1 (*Eucalyptus oreades*) was recorded only in undermined swamps (Appendix S6). There was strong evidence of

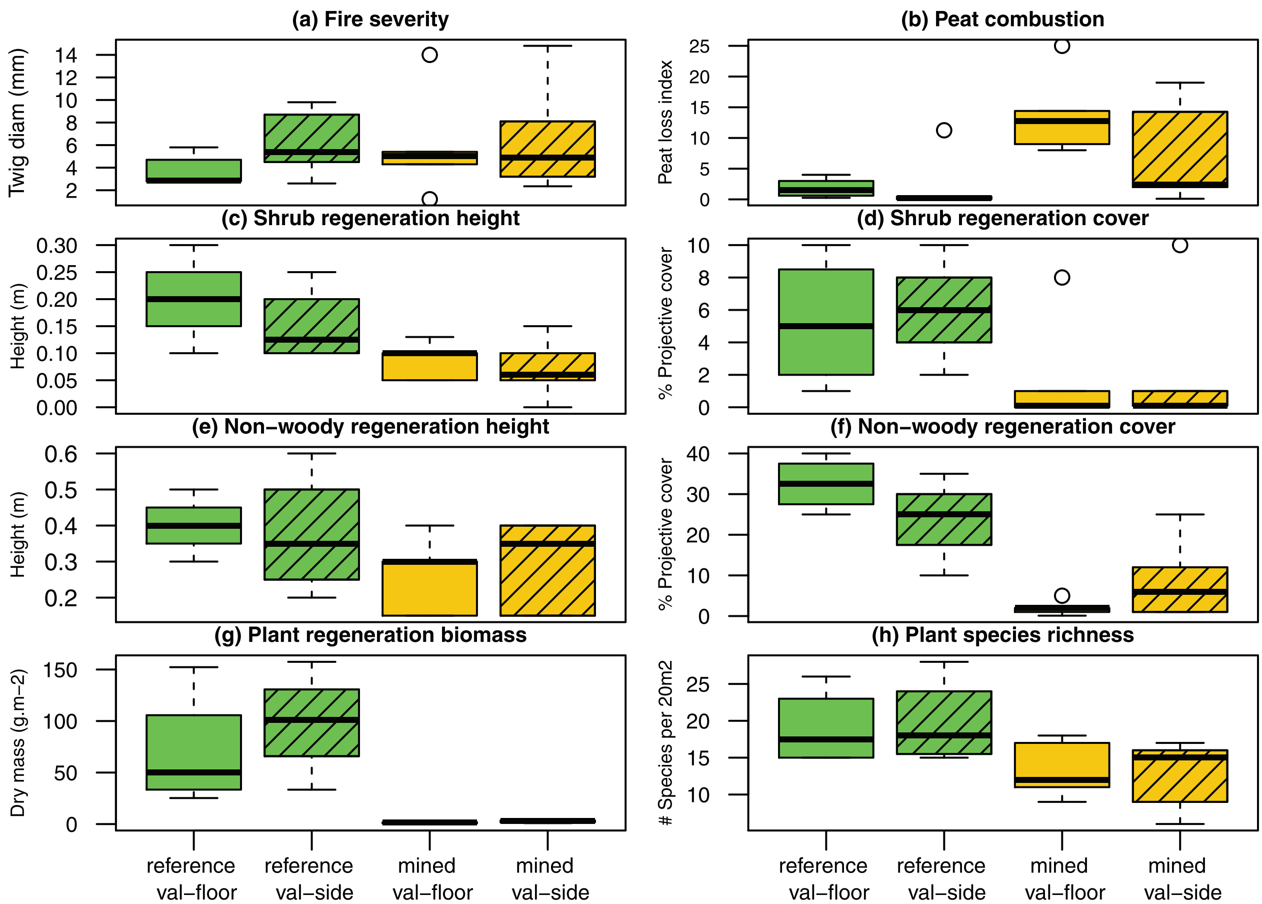

FIGURE 4 Comparative exposure of reference and undermined swamps on their valley floors (val-floor) and sides (val-side) to (a) fire severity based on the minimum diameter of remaining shrub twigs or branches and ecosystem responses based on (b) peat combustion index, (c) height of regenerating shrubs, (d) cover of regenerating shrubs, (e) height of regenerating nonwoody plants, (f) cover of regenerating nonwoody plants, (g) regenerating plant biomass, and (h) plant species richness (solid line in boxes, median; box, limit of upper and lower quartile; whiskers, maximum and minumum values; circles, outliers). All variables measured 10 weeks after the fire, except plant species richness, which was based on pooled species recorded 10 weeks (early autumn) and 11 months (late spring) after fire

differences in abundance between mining treatments in 3 species ($p << 0.01$), moderate evidence of differences in 7 species ($p < 0.05$), weak evidence of differences in a further 4 species ($p < 0.1$), and weak evidence of differences due to mining on 1 of the landforms (interaction term $p < 0.1$). Thus, just over half of the species examined showed some evidence of mining effects. Nine of the 43 species examined showed evidence of differences in abundance between landform types (Appendix S6).

There was very strong evidence of an interactive effect of mining treatment and landform on fire-related plant mortality ($z = 8.66$, $p < 0.0001$) (Appendix S5). Almost all (95% CI: 86–99) detectable prefire established plants were killed by fire on valley floors of undermined swamps compared with only 2% (1–7) in unmined reference swamps, whereas fire mortality on valley sides of undermined swamps was 66% (42–84) compared with 21% (9–41) in unmined reference swamps (Figure 6)). Mortality responses varied among the 6 species included in the model (variance 1.421 [SD 1.192]).

There was strong evidence that mining reduced postfire seedling recruitment compared with unmined swamps (deviance = 74.9, $p = 0.004$) (Appendix S7), but neither landform main effects ($p = 0.45$) nor the interaction term ($p = 0.21$) was important in the model. Overall, the density of emerged postfire seedlings in undermined swamps was 11.9 m^{-2} (SE 1.4) compared with 56.0 m^{-2} (6.9) in unmined reference swamps. Two species were recorded only in reference swamps, 1 was recorded only in undermined swamps (*E. oreades*), 2 species exhibited moderate evidence of differences ($p < 0.05$), and 2 species exhibited weak evidence of differences ($p < 0.1$) (Appendix S7).

Skink abundance declined approximately to zero in undermined swamps but remained extant without strong trends in unmined reference swamps (mining:time interaction $t = 5.17$, $p < 0.0001$) (Figure 7; Appendix S7); rainfall accounted for a small component of interannual variation ($t = 2.57$, $p = 0.010$). No skinks were detected in any of the undermined swamps in 2022.

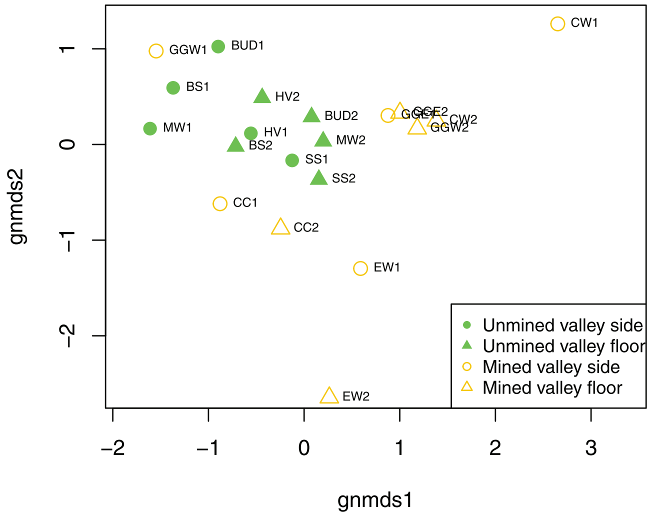

FIGURE 5 A global nonmetric multidimensional scaling ordination showing differences in species composition between undermined swamps and unmined reference swamps, as well as distinctions between landforms (letter number combinations, defined in Appendix S2)

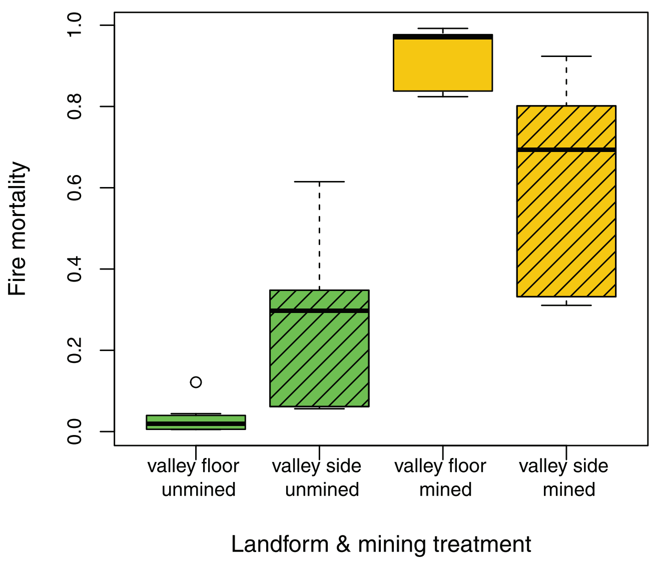

FIGURE 6 Variation in mortality rates of 6 detectable and abundant resprouting plant species in relation to landform and mining treatments (solid line in boxes, median; box, limit of upper and lower quartile; whiskers, maximum and minimum values; circles, outlier. Mortality estimates predicted from a mixed binomial linear model with species as a random factor (see METHODS)

DISCUSSION

Diminution of resilience precedes ecosystem collapse

Ecosystem responses to wildland fire differed markedly between swamps that had been exposed to underground mining and reference swamps that had not been exposed to mining. These differences in response were expressed in a wide range of ecosystem indicators, even though undermined and reference swamps experienced similar climatic conditions and similar fire severity (as estimated by several metrics). Relative to unmined reference swamps, undermined swamps showed greater loss of peat via substrate combustion, reduced cover of regenerating vegetation (both woody and nonwoody components), reduced height of regenerating shrubs, reduced biomass of regenerating vegetation, reduced postfire plant species richness and abundance, altered plant species composition, increased mortality rates of woody plants, reduced postfire seedling recruitment, and local extinction of a hydrophilic fauna species. These differences indicate transformational changes in structure, composition, and function consistent with ecosystem collapse in swamps exposed to underground mining (Figure 8). The autogenic postfire recovery process evident in unmined reference swamps was disrupted in the undermined swamps, resulting in a new system with more slowly growing, sparser, and shorter vegetation, with much reduced abundance of hydrophilic species that characterize functional swamps and entry of nonhydrophilic species including trees and nonnative taxa.

The soil moisture data indicated that undermined swamps underwent a change in hydrological regime soon after coal seam extraction but prior to the passage of fire. This prior change in a key ecosystem driver (groundwater hydrology) apparently predisposed the swamps to major fire impacts across the range of ecosystem indicators examined. Similarly, surface ditching resulted in greater peat consumption in burned fens, relative to burned undrained reference fens (Turetsky et al., 2011). We therefore conclude that our results support our model of ecosystem collapse (Figure 1) in which a stressor on ecosystem hydrology (longwall mining) diminishes the resilience of an ecosystem to a perturbation (wildland fire). The postfire responses of reference swamps suggest that, in the absence of the stressor, the ecosystems maintain resilience to the perturbation, enabling them to return to their ecological basin of attraction (Folke et al., 2004).

Although we did not explicitly examine climate change, our results have important implications for understanding its role in the sustainability of upland swamp ecosystems. Even though longwall mining diminishes resilience by reducing substrate permeability, climate change may diminish resilience to fire by amplifying hydrological stress through increasing evapotranspiration relative to precipitation. Ecosystem responses to climate change may be delayed and subject to greater fluctuation (due to interannual weather cycles) compared with responses to longwall mining, but the transformation outcomes are likely to be similar, given the climatically marginal conditions for peat-forming ecosystems on mainland Australia. Although climate change is a pervasive stressor subject to ecological lags and inertia of Earth systems, longwall mining is a localized stressor, responsive to relatively short-term deterministic management decisions about where and how to extract coal. The 2 stressors act together (within mining footprints) or climate change acts alone (beyond mining footprints). Therefore, it should be possible to reduce and delay the total loss of resilience by managing the short-term stressor (longwall mining), allowing time for

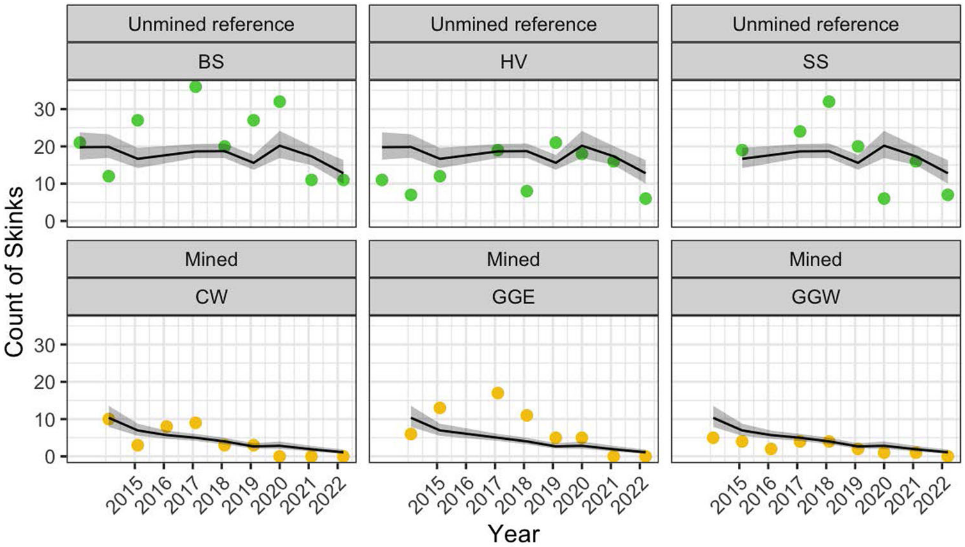

FIGURE 7 Trends in captures of *Eulamprus leuraensis* (Blue Mountains water skink), an obligate hydrophilic animal species, in 3 unmined reference swamps (top row) and 3 undermined swamps (bottom row) (shading, 95% confidence intervals estimated using a nonparametric case bootstrap coupled with individual residual bootstrap for the range of rain values across all years)

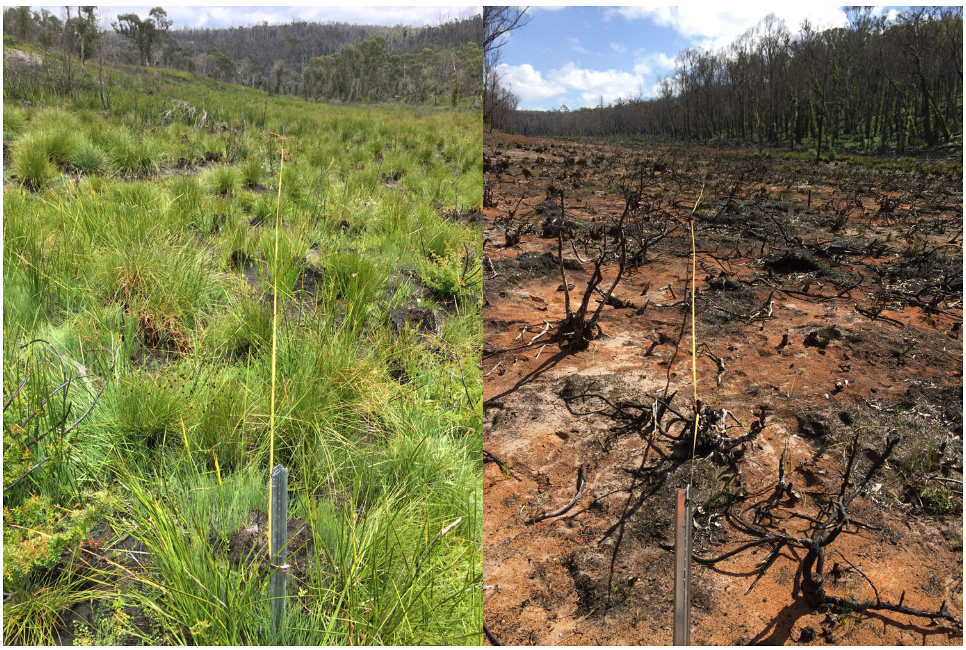

FIGURE 8 Resilient response to fire at Happy Valley reference swamp (left) and ecosystem collapse after underground mining and fire at Carne West swamp (right). Both photos taken during the November 2020 survey, 11 months after bushfires in December 2019 (photo by D.A.K)

climate change mitigation measures to take effect on the long-term stressor (climatic water deficit).

Consequences of ecosystem collapse

Concerns about the effect of underground longwall mining on groundwater and surface hydrology have been discussed for some time (Krogh, 2007; NSW Scientific Committee, 2005). Knowledge was initially circumstantial, built on post hoc observations of multiple independent drying and erosion events related to longwall mining (and associated subsidence, bedrock cracking, and surface warping) that occurred in months and years prior to those events (Krogh, 2007). A review of remedial treatments found that none were successful in restoring the hydrology of affected swamps (Commonwealth of Australia, 2014). Long-term monitoring also showed no evidence of autogenic recovery of hydrological function over 5 years after mining (Mason et al., 2021).

The consequences of wetland ecosystem collapse are substantial for both biodiversity and ecosystem services. The Newnes Plateau Shrub Swamps belong to a global ecosystem functional group (TF1.6 Boreal, temperate and montane peat bogs [Keith et al., 2022]) that has a very limited distribution in the Southern Hemisphere, with 0.33% of the global distribution in Australia (data from https://global-ecosystems.org/analyse?biome=TF1&regionId=ADM_164), where climatic conditions are marginal for peat development. The Newnes Plateau Shrub Swamps belong to 1 of 4 such ecosystem types currently listed as endangered ecological communities under national biodiversity legislation. The trends documented here indicate accelerating decline in its status. Biodiversity declines are also expressed at the species level. The Newnes swamps host a range of locally endemic taxa and many that occupy narrow ecological niches that are predisposed to elevated extinction risks from hydrological change, including several already listed as threatened under national legislation (Krogh et al., 2022). At landscape scales, peatland ecosystems are critical to supply of multiple ecosystem services, including carbon sequestration (Cowley & Fryirs, 2020), regulation of stream flow, mitigation of droughts and floods (Cowley et al., 2018; Young, 2017), supply of drinking water (Krogh, 2007), and maintenance of riverine and estuarine recreational waters. These values, together with the irreversibility of ecosystem collapse, underscore the need for prediction and early warning of ecosystem collapse (Scheffer et al., 2009), as well as precautionary decision-making to ensure ecologically sustainable development (Mason et al., 2021).

Early diagnosis and risk reduction for collapse-prone ecosystems

Early detection of decline from time-series observations could inform intervention to prevent ecosystem collapse (Scheffer et al., 2009). Indicators of critical slowing show promise for early warning in ecosystems exposed to slowly changing drivers that may generate abrupt changes in ecosystem state (Dakos et al., 2015). The collapse of Newnes swamps, however, involves strong stepwise change in a stressor that initiates rapid change in a hydrological driver (similar to mechanism 'f' of Dakos et al. [2015]), which is unlikely to be detected by critical-slowing indicators. Even if critical slowing were detected from a hydrological time series, no management action could reverse hydrological decline after mining had initiated it (Commonwealth of Australia, 2014). Additionally, the in situ methods required to monitor proximal state variables may impose operational constraints on acquisition of high-density time series suitable for early detection of critical slowing. Resourcing and slow response rates limit applications of critical-slowing indicators except in commercially exploited ecosystems, such as fisheries or where remote sensing can provide data streams of informative and sensitive indicators of collapse (Bolt et al., 2021).

We suggest a 4-step strategy for sustaining ecosystems: step 1, diagnose potential mechanisms and likely causes of collapse; step 2, reduce risks through preventative actions that address causal drivers and maintain resilience; step 3, detect, delay, and ameliorate expression of symptoms of collapse; and step 4, restore ecosystem resilience. Early detection of collapse from time series of ecosystem observations has a role in step 3, depending on the outcome of steps 1 and 2.

Diagnosing the potential mechanisms of collapse (step 1) has 2 components. The first is a qualitative diagnosis or "imaginative synthesis" (Keith et al., 2011) to identify alternative ecosystem states, key components, and the causes, effects, and dependencies of change. Experiential knowledge and qualitative diagrammatic models (e.g., Figure 2) are powerful tools for such diagnostic synthesis (Keith et al., 2015). This should reveal suitably proximal and sensitive state variables to examine ecosystem responses to the hypothesized stressors.

The second component of diagnosis is to quantify the thresholds in drivers and state variables that mark a state change and inform timely preventative action. They may be estimated by probing the system experimentally, accumulating and synthesizing case histories, or by drawing on indirect evidence from similar ecosystems as operational constraints permit (Keith et al., 2011; Walter & Holling, 1990).

Ecosystems that collapse locally (such as in individual peatlands) or through reversible processes (such as in small lakes) offer more scope than singular systems to estimate thresholds by observation (Scheffer et al., 2009). For singular systems, such as ocean upwelling zones, extrapolation from models and learnings from related ecosystems will be the primary basis for threshold estimation (Bland et al., 2018). For upland swamps, case histories show that collapse has occurred locally across a range of longwall mine designs that vary in panel width (Young, 2017) and that no-collapse outcomes may require mining exclusion zones (Mason et al., 2021).

Risk reduction and impact avoidance (step 2) is a preventative measure that is the only viable means of achieving ecosystem sustainability where collapse may be irreversible over timescales practicable for ecosystem management. Alternative strategies should be deployed through active adaptive management and monitored and evaluated to learn by doing about the most effective risk reduction options (Walter & Holling, 1990; Williams, 2011). Alternative risk-reduction strategies that warrant investigation for our study system may involve mining exclusion zones of varying sizes and configurations or different partial extraction designs with substantial seam retention (Mason et al., 2021). More generally, to reduce risk in other ecosystems, managers can explore alternative fire regimes (e.g., in savannas and other fire-affected ecosystems), varied levels and patterns of harvest (e.g., in fisheries and other trophically regulated systems), varied pollution regulations (e.g., in stream or lake catchments), and so forth.

It may be possible to devise management strategies that delay or reduce the expression of symptoms of ecosystem decline (step 3). By prolonging the time that ecosystems support biodiversity and supply services, these impact minimization strategies can complement, rather than substitute for, risk-reduction strategies. Forestalling the expression of collapse may provide opportunities for lagged remedial measures to take effect, for interventions to secure translocated or ex situ populations of affected species, or to develop and implement new restoration technologies. For example, the most severe symptoms of ecosystem collapse in Newnes swamps occurred abruptly after fire, even though declines in hydrological function, carbon sequestration, and biodiversity were set in motion soon after coal seam extraction. Fire exclusion may not have avoided collapse of the peatlands, but would have slowed rates of carbon emission from peat and prolonged survival of standing plants, their root mats, and seed banks, providing material for translocation, extending the stability of sediments and the potential for regeneration if new technologies for restoring hydrological conditions were developed in future.

Finally, ecosystem restoration could be an effective strategy where the mechanism of ecosystem collapse is reversible. Reversal may occur autogenically or in response to an environmental trigger and may be promoted or accelerated by restoration management. However, restoration techniques are still in their infancy in many ecosystem types, and there are relatively few examples of fully successful ecosystem restoration outcomes (Gann, et al., 2019). None have been demonstrated for peat-accumulating wetlands affected by underground mining (Commonwealth of Australia, 2014). At Newnes, for example, remediation measures failed to restore 1 of our study sites (East Wolgan swamp) (Young, 2017). Where the reversibility of collapse or the effectiveness of restoration techniques is uncertain, preventative risk reduction will be a superior strategy for sustaining ecosystem biodiversity and function.

Ecosystem collapse may be viewed in the context of a broader socioecological lens (Cumming & Peterson, 2017) in which economic norms have driven markets for coal and development of cost-efficient longwall extraction methods. A transition is underway to a clean energy future, driven by new social attitudes, economic imperatives, and emergence of cost-effective alternative energy technology. Consequently, the demand for coal is declining. Implementing low-impact mine designs with suitable exclusion zones during the transitional phase, trading off marginal increments in the cost of coal extraction, should achieve large benefits in ecosystem risk reduction to maintain the biodiversity and ecosystem services that are supported by upland swamp ecosystems. The alternative pathway, maximizing coal production and its economic outputs prior to inevitable industry collapse, will cause irreversible ecosystem collapse and permanent loss of associated biodiversity and ecosystem services.

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SUPPORTING INFORMATION

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

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