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If the trees burn, is the forest lost? Past dynamics in temperate forests help inform management strategies

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Forest dynamics are driven by top-down changes in climate and bottom-up positive (destabilizing) and negative (stabilizing) biophysical feedbacks involving disturbance and biotic interactions. When positive feedbacks prevail, the resulting self-propagating changes can potentially shift the system into a new state, even in the absence of climate change. Conversely, negative feedbacks help maintain a dynamic equilibrium that allows communities to recover their pre-disturbance characteristics. We examine palaeoenvironmental records from temperate forests to assess the nature of long-term stability and regime shifts under a broader range of environmental forcings than can be observed at present. Forest histories from northwestern USA, Patagonia, Tasmania and New Zealand show long-term trajectories that were governed by (i) the biophysical template, (ii) characteristics of climate and disturbance, (iii) historical legacies that condition the ecological capacity to respond to subsequent disturbances, and (iv) thresholds that act as irreversible barriers. Attention only to current forest conditions overlooks the significance of history in creating path dependency, the importance of individual extreme events, and the inherent feedbacks that force an ecosystem into reorganization. A long-time perspective on ecological resilience helps guide conservation strategies that focus on environmental preservation as well as identify vulnerable species and ecosystems to future climate change.

This article is part of the theme issue 'Climate change and ecosystems: threats, opportunities and solutions'.

1. Introduction

Projected changes in climate and land-use pose enormous challenges for conservation efforts that seek to maintain natural ecosystems and the services they provide [1]. Unlike past strategies that often focused on the preservation of historical landscapes, conservation planning now recognizes the dynamic nature of ecosystems as variable networks controlled by interactions that operate across time and space [2,3]. This paradigm shift from a stationary, balance-of-nature perspective towards a more dynamical view of ecological change [4] has deep roots in palaeoecology, a discipline that examines long-term interactions between species and their environment. Proxy records of past environmental dynamics show that landscapes have varied through time and, rather than the exception, ecological reorganizations are the norm [5,6]. In this paper, we draw on palaeoecology to illustrate the changing role of fire in forests to promote stable, unstable and disequilibrium conditions, as well as its potential to trigger regime shifts. Our examples come from the northwestern USA, Patagonia, Tasmania and New Zealand, where pollen and charcoal data describe vegetation–fire–climate linkages since the last ice age, approximately 20 000 years ago. Our objective is to provide a long-term context for evaluating current conditions and highlight the unique contribution of palaeoecology towards understanding the dimensions of ecological resilience in ways that can guide conservation efforts to accommodate change [7–9].

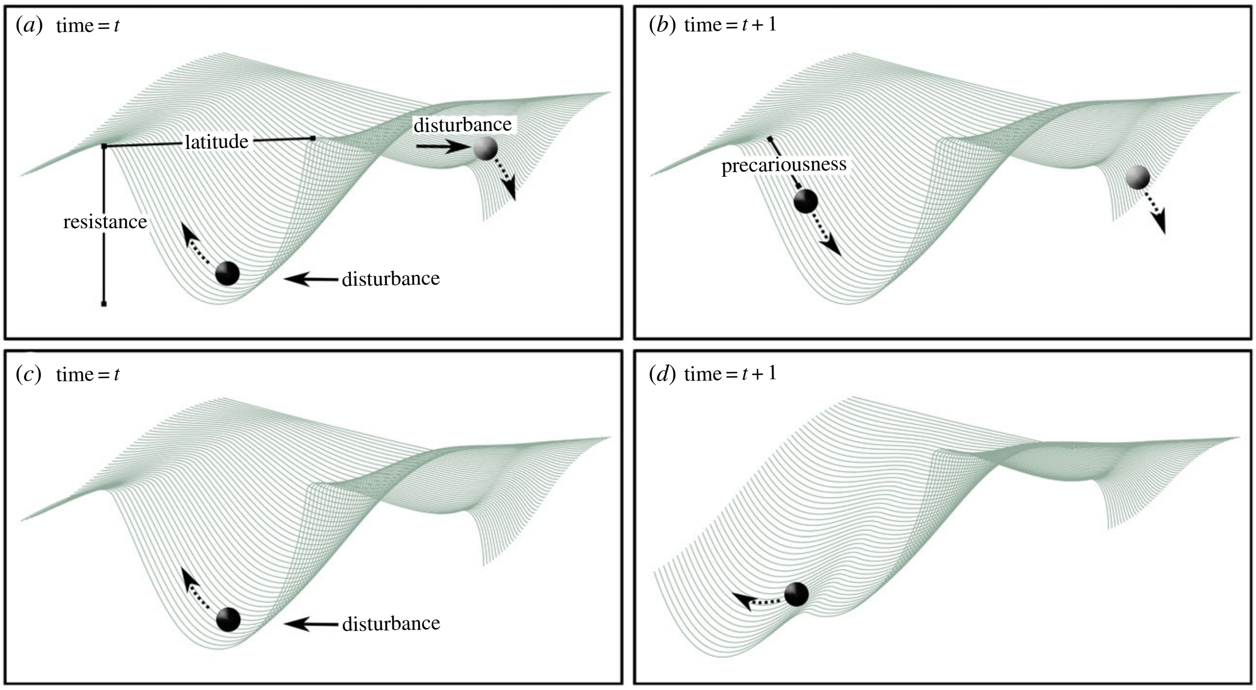

Figure 1. Ball-and-cup diagram showing systems in stable (black circle) and unstable (grey circle) equilibrium at (*a*) time = *t* and (*b*) time = *t* + 1. A system in disequilibrium at (*c*) time = *t* and (*d*) time = *t* + 1. Note that while in (*b*) only the position of the ball changes (i.e. invariable parameters), the ball moves as a consequence of changes in shape of the cup in (*d*) (i.e. varying parameters). (Online version in colour.)

2. Forests as complex, dynamic systems

Complexity refers to systems (physical, biological or social; natural or artificial) whose dynamics are driven by various interdependent agents and their interactions [10]. Forests satisfy this condition in that their trajectory is driven by a combination of top-down controls and bottom-up biophysical feedbacks [11]. Climate is usually considered the primary top-down control or boundary condition that governs the distribution and composition of ecosystems, and bottom-up elements include the physical template, biotic and abiotic interactions, and disturbance regime, including that caused by humans. Within a range of top-down controls (i.e. whether the species-specific climate requirements are met), ecosystem variability is largely shaped by bottom-up forcing [12]. Suitable climate consequently emerges as a necessary condition for vegetation establishment and survival but, by itself, does not provide a sufficient set of mechanisms to explain the distribution and behaviour of plant communities [13,14].

We draw on a resilience theory framework, facilitated by the ball-and-cup analogy ([15] and references therein), to understand forest dynamics over centuries to millennia. The ball depicts the state variable, which in this study, is vegetation composition as inferred from pollen data. The cup (stability basin) can be thought of as the n-dimensional hypervolume defined by a suite of states and resulting feedbacks under which the structure and relationships within the system are preserved. Disturbances push the ball and trigger interactions that modify the distance between the ball and the edge of the cup (i.e. alter the precariousness of the ecosystem).

The magnitude of disturbance that can be tolerated before a system moves into a different region of the state-space (i.e. regime shift; [16]) depends on the dimensions of the stability basin, disturbance history and boundary conditions. Contingent on ball-cup-disturbance relationships, three basic scenarios are possible. Resilient ecosystems may reside in a stable equilibrium if the height and width of the cup are constant (known as resistance and latitude, respectively), and they are able to recover from disturbance through negative, stabilizing feedbacks [17]. Alternatively, the ball may move further away from its initial location when the dominant feedbacks are positive, which will possibly lead to unstable equilibrium. Finally, if the shape of the cup changes over time (i.e. variable external forcing such as climate change), the ball will tend to dynamically adapt to the new configuration (i.e. disequilibrium). Thus, resilience is a fundamental property emerging from the relationship between disturbance and the state of the ecosystem (figure 1).

This heuristic representation of a trajectory can be formalized and applied to any system whose state changes over time, such as a forest. A discrete-time model with a single-state variable will be in dynamic equilibrium if

$$x_{(t+1)} = f(x_t) \text{ and } \left|\frac{\mathrm{d}f(x_t)}{\mathrm{d}x_t}\right| < 1. \qquad (2.1)$$

Therefore, a system exhibits dynamic equilibrium if (i) it has memory (e.g. the size of a population depends on its previous size); (ii) its state fluctuates (e.g. population size is variable owing to changes in recruitment and mortality) and (iii) it does not experience net change over a predefined spatiotemporal domain (e.g. the structure and composition of the forest remain essentially unchanged). This representation assumes that interactions are scale-dependent and self-contained; state variables oscillate within the stability basin, and parameters are invariable and constrain system dynamics. The solution of equation (2.1) can be negative or positive, representing a system in stable or unstable equilibrium, respectively [18].

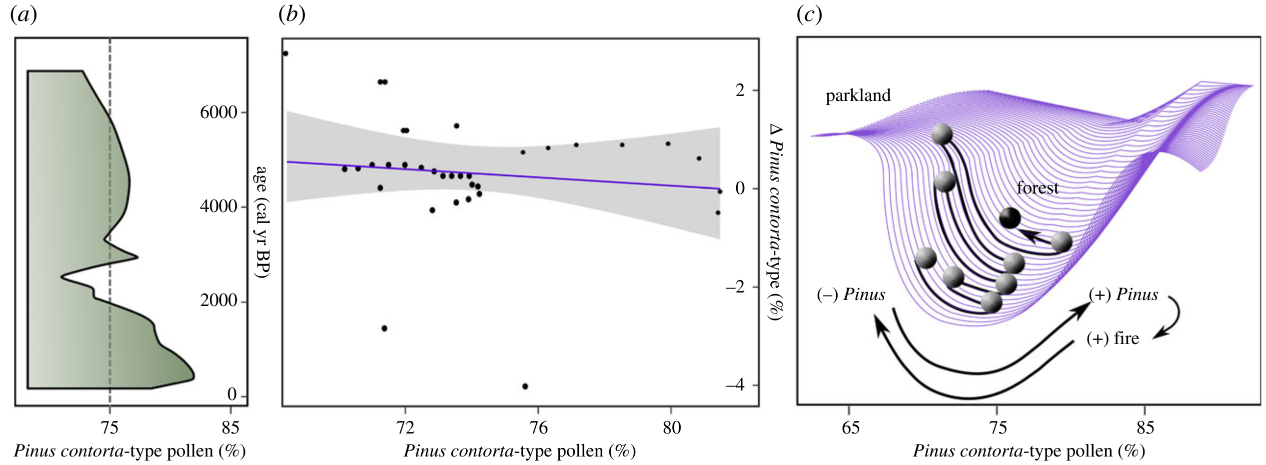

Figure 2. A system in stable equilibrium. (*a*) Abundance of *Pinus contorta* at Cygnet Lake (44.7° N; USA) during the last 7000 years inferred from pollen percentage data [19]. (*b*) Changes in pollen percentages between times $t + 1$ and t as a function of pollen abundance at time t. The nearly horizontal, negative regression line (slope = −0.05; equation (2.1)) indicates that *Pinus* populations were in stable equilibrium. (*c*) Graphical representation of *Pinus* population dynamics. The bowl depicts the stability basin, and the grey balls encode the values assumed by the state variable (i.e. pollen percentages). The temporal trajectory is shown with a black line and arrow and the black ball shows the present-day configuration. (Online version in colour.)

3. Systems in stable equilibrium (ball in the basin): if the trees burn, the forest will probably persist

Stable systems tend to overcompensate when returning to their equilibrium point, meaning that they are equally likely to display positive or negative anomalies with respect to their mean state and, as a consequence, feature no net change (figure 1*a*,*b*). Evidence of this dynamic in the palaeoecological record is shaped by the characteristics of particular taxa and the biophysical setting as well as by the feedbacks resulting from long-term fire–climate interactions. For example, pollen data register the establishment of *Pinus contorta* parkland in the Greater Yellowstone Ecosystem in northwestern Wyoming (44.7° N; GYE) at 11 000 cal yr BP (cal yr BP = calibrated years before AD 1950), probably favoured by postglacial warming [19]. The initially open vegetation developed into closed forests as moisture increased at 7000 cal yr BP; the structure and composition of the forests have remained relatively unchanged since then (equation (2.1); figure 2).

The reason for the long-term stability of *Pinus contorta* forest is probably threefold. First, model simulations suggest that climate variability in the last 7000 years was relatively small (less than 2°C; [20]) and within the tolerance of the species. Second, the infertile, well-drained rhyolite substrates of central Yellowstone limited establishment of other conifers, thus facilitating *Pinus contorta* dominance. In similar but non-rhyolite settings in Yellowstone, *Picea engelmannii*, *Abies lasiocarpa* and *Pinus albicaulis* have co-dominated [19,21]. Third, *Pinus contorta* has great resilience to fire, as evidenced by charcoal data showing a sixfold range in fire frequency over the last 11 000 years with minor, reversible changes in population size [22]. Intrinsic traits of *Pinus contorta* (e.g. adaptation to climate variability and fire, which result from a combination of serotiny and rapid seedling growth [23]) and extrinsic factors (e.g. infertile substrate and little climate variability relative to the tolerance of the species) have conferred stability on this forest type in the Yellowstone region. Stability will probably persist until warming limits the capacity of *Pinus contorta* to regenerate or a shift in the fire regime alters post-fire recovery.

Similar edaphic constraints also help explain the heterogeneous conifer forests in the Klamath Mountains of southwestern Oregon and northwestern California (USA). On fertile substrates in this region, pollen records suggest pronounced shifts in forest composition over the last 9000 years in response to changes in climate and fire activity. Conversely, on adjacent infertile ultramafic soils, there has been little variability in vegetation despite similar shifts in climate and disturbance [24]. These contrasting histories highlight the importance of bottom-up controls on biodiversity and suggest that forests adapted to the extreme nutrient limitations of ultramafic substrates in the Klamath region possess larger climate envelopes and greater capacity to reorganize after disturbance than those with higher diversity and nutrient demands. We note that this behaviour is ecosystem-specific and dependent on the prevailing fire–vegetation feedbacks, as well as the legacy of forest management and land-use characteristic of each location (e.g. [25]).

Forests in Patagonia have also exhibited compositional stability over millennia. Pollen data from the east side of the Andes (44° S) indicate that *Nothofagus pumilio* forest was established at 7000 cal yr BP and remained virtually unchanged until Euro-American settlement in eighteenth century [26]. *Nothofagus pumilio* reproduces under a large range of climate conditions, but successful recruitment requires light openings created by small fires, windstorms, landslides and avalanches [27]. However, with European settlement, fires have become larger and more severe, and extensive livestock grazing has reduced seedling establishment and regeneration, leading to replacement by shrubs [28]. Despite a long history of *Nothofagus pumilio* forests in central Patagonia, stability and even permanence of this forest association seem in jeopardy [29].

4. Systems in unstable equilibrium (ball on the edge): if the trees burn, the forest may eventually collapse

Instability occurs when disturbance triggers unidirectional displacement of the system through a series of positive

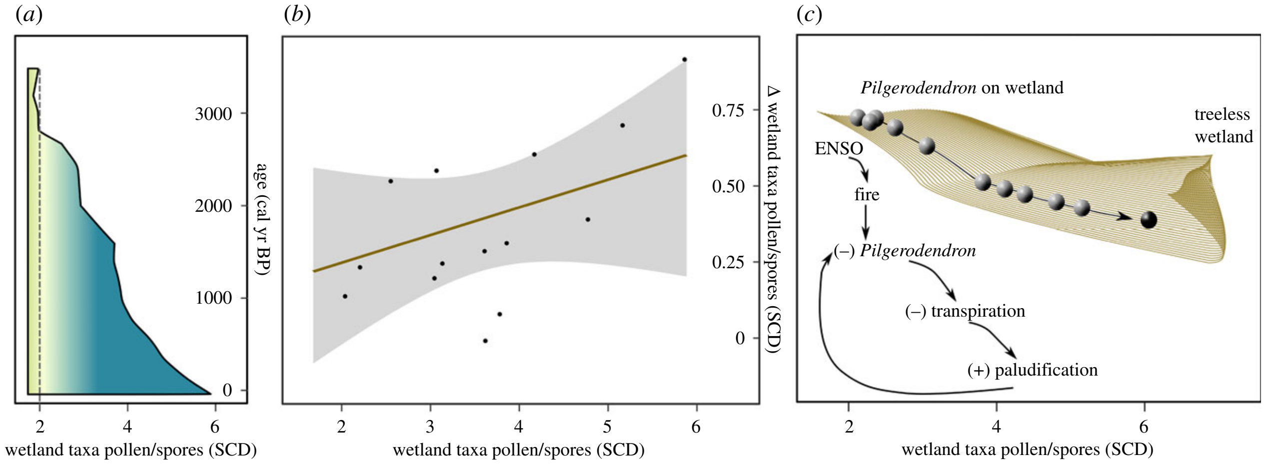

Figure 3. A system showing instability. (*a*) Wetland dynamics at Mallín Casanova (47.4° S; Chile) inferred from squared-chord distances (SCD) between every pollen sample and the first sample of the record (9500 cal yr BP). SCDs were based on a dissimilarity matrix produced for all aquatic and wetland taxa and interpreted as temporal changes in wetland composition [30]. (*b*) Changes in SCD between times $t + 1$ and t as a function of SCD at time t. The nearly horizontal, positive regression line (slope = 0.22; equation (2.1)) indicates that the wetland was in unstable equilibrium. (*c*) Graphical representation of wetland dynamics. The surface depicts the stability basin, and the grey balls encode the values adopted by the state variable (i.e. SCD). The temporal trajectory is shown with a black line and arrow and the black ball shows the present-day configuration. Note that the shift in the fire regime resulted from changes in climate and/or human ignitions, but the hydrological response that followed was driven by internal feedbacks. (Online version in colour.)

feedbacks (figure 1*a*,*b*). An example of interactions leading to self-amplifying ecological reorganization comes from southern Chile. Mallín Casanova (47.4° S) is a broad wetland surrounded by rainforests of *Nothofagus pumilio* and *Pilgerodendron uviferum*. Radiocarbon-dated reconstructions show that the modern bog developed at 5800 cal yr BP, probably in response to the onset of wetter conditions that impacted all of Patagonia [30]. Approximately 2000 years ago, charcoal data indicate that fires became more frequent. Although upland *Nothofagus*-dominated forest remained relatively unchanged, the abundance of *Pilgerodendron* around the wetland sharply declined, setting up a positive feedback loop at lower elevations. Reduced evapotranspiration on the wet valley floor led to paludification, lowered the pH of already acidic soils and limited seedling recruitment. This shift in the fire regime is attributed to El Niño-Southern Oscillation (ENSO) intensification [31] and/or human ignitions, but the hydro-ecological response that followed was driven by biophysical interactions (figure 3). The site's history, therefore, suggests that positive feedbacks, triggered by a change in fire, led to progressive deforestation and altered the hydrology of the basin.

Owing to their self-amplifying nature, positive feedbacks may result in regime shifts, even in the absence of external forcing. *Nothofagus dombeyi* and *Austrocedrus chilensis* co-dominate the mixed forests on the eastern flank of the Andes (41° S; Argentina). These forests lie at the drier end of a moisture gradient, in which *Nothofagus* is replaced by *Austrocedrus* as conditions become more xeric. Pollen data show that these two species traded dominance for the last 5000 years, with humid periods sustaining *Nothofagus*, and drier times favouring *Austrocedrus*. Under these extreme conditions, ecosystems were in stable equilibrium [32].

At intermediate moisture levels, both species approached their respective limits of tolerance, and the relative proportion of either taxon depended on positive feedbacks involving fire. *Austrocedrus*, a shade-intolerant, slow-growing conifer, was able to outcompete *Nothofagus*, a fast-growing evergreen hardwood, only when disturbed by small, low-severity fires. These fires allowed recruitment of grasses that supported subsequent surface fires. Conversely, stand-replacing fires facilitated *Nothofagus* dominance, and the higher water content of *Nothofagus* foliage constrained burning to dry years, promoting a positive feedback between *Nothofagus* and high-severity fires [14]. The alternating responses in northern Patagonia highlight the role of fire in driving ecosystem dynamics at the boundaries between vegetation communities with different climate tolerances, and suggest that conservation strategies to preserve *Austrocedrus* should include maintenance of surface fires [33].

Forest-grassland boundaries from around the world are subject to similar fire-mediated shifts between stable states (i.e. forested and non-forested). Although precipitation is a good predictor of vegetation structure, tree cover in areas with mean annual precipitation of 1000–2500 mm is bimodal. As a result, both forests and savannahs persist in large areas of Amazonia, Congo and Australia under similar precipitation regimes [32,34]. In these subtropical zones, forests prevail in association with the near-absence of fire while burning is ubiquitous in savannahs [35]. Fire, then, differentiates the stability basins where climate can deterministically support the two vegetation types. The emerging tipping point can be formalized as the unstable state between stability basins (i.e. forest and savannah) where positive vegetation–fire feedbacks necessarily induce a self-propagating regime shift.

Regime shifts have also been triggered by unprecedented disturbance events. The ecological history of northwestern Tasmania (41.6° S) reveals that *Nothofagus-Athrotaxis* montane rainforest reached its greatest extent of the last 20 000 years between 9000 and 5000 cal yr BP [36]. Charcoal data indicate that fire activity was low during this period and that rainforests were resilient to this level of disturbance. Increased aridity during the last 5000 years is evidenced by the decline in pollen of *Nothofagus* and increase in that of sclerophyllous taxa, including *Eucalyptus*. This trend was hastened at 3800 cal yr BP by a major fire episode, which lay well outside the previous range of variability and apparently exceeded rainforest resilience [37]. Although fire activity returned to

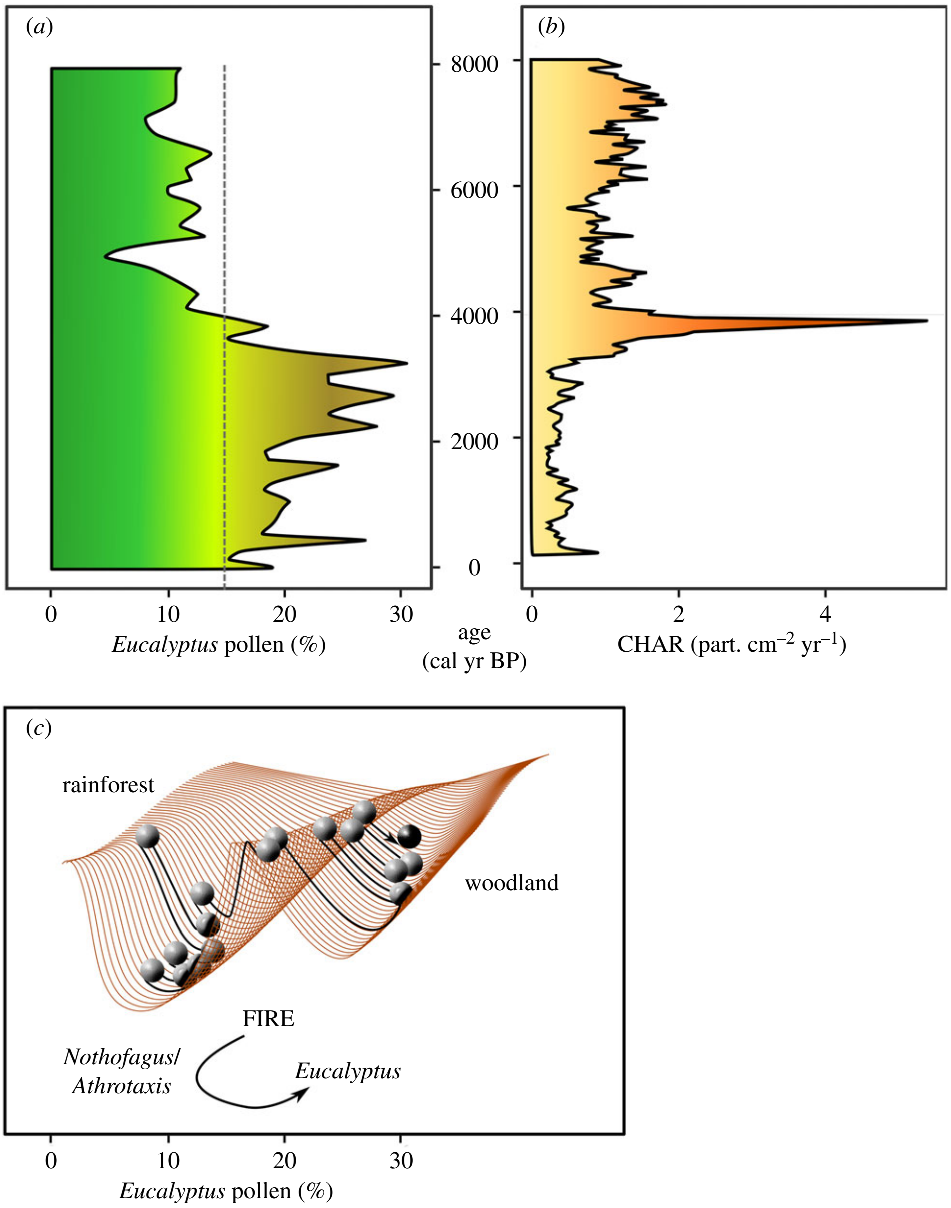

Figure 4. Vegetation and fire history of Wombat Pool (41.6° S; Tasmania) during the last 8000 years. (*a*) *Eucalyptus* pollen percentages show the relative abundance of *Eucalyptus* and *Nothofagus*, and indicate an abrupt shift in vegetation at 3800 cal yr BP [37]. (*b*) Charcoal accumulation rates (CHAR) are a proxy of fire activity and reveal the unprecedented magnitude of the fire episode at 3800 cal yr BP. (*c*) Graphical representation of vegetation dynamics. The bowl depicts the *Nothofagus* forest and *Eucalyptus* woodland stability basins, and the grey balls encode the values adopted by the state variable (i.e. pollen percentages), with its temporal trajectory shown by the black line and arrow. The black ball shows the present-day configuration. (Online version in colour.)

previous levels soon after, montane rainforest never fully recovered and sclerophyllous taxa dominate to the present day (figure 4).

Failed rainforest recovery after the 3800 cal yr BP fire suggests that the change in Tasmania was possibly hysteretic. Hysteresis is a consequence of the history-dependence of systems characterized by different pre- and post-disturbance equilibrium points. As a result, the trajectory of the state variable cannot be reversed by simply suppressing disturbance, and systems may be easily forced into configurations from which recovery may prove difficult, slow or even impossible [18]. Available palaeoenvironmental data do not allow us to determine whether the vegetation shift was irreversible but strongly suggest that present forest composition is a legacy of a disturbance episode on an ecosystem that was already approaching a tipping point owing to drying conditions (i.e. low precariousness; [35,36]). A regime shift triggered by a large fire episode and heightened by slowly declining moisture levels raises concerns for conservation in the face of recent high fire activity and future climate projections in Tasmania [38].

The destabilizing effect of unprecedented disturbance is also evident in South Island, New Zealand, where the native forests of *Fuscospora*, *Lophozonia* and podocarps (*Podocarpus*, *Prumnopitys*, *Dacrycarpus*) had little adaptation to fire. Following the arrival of people in AD 1280, approximately 50% of the forest was lost and, in some places, repeated burning led to deforestation within decades [39,40]. The rapid and hysteretic disappearance of closed-canopy forest is attributed to positive feedbacks that favoured more flammable early successional shrubs and created a situation in which fire begets fire [41]. Returning to native forest in New Zealand poses a difficult conservation challenge that requires not only complete fire suppression in remnant stands but also removal of mammalian seed predators, strategic planting of seedlings to support nucleation processes and the reinstatement of pollinators [41].

5. Systems in disequilibrium (ball in a changing cup): even if the trees do not burn, the forest may collapse

Palaeoecological data suggest that disturbance plays a catalytic role when ecosystems are in equilibrium. However, there have also been times when vegetation change was so rapid and sustained that equilibrial conditions were exceeded (i.e. $|df(x_t)/dx_t| > 1$; figure 1*c*,*d*), and variability was brought about by shifting boundary conditions. Perhaps the most dramatic and widespread period of disequilibrium is described by the pronounced ecological changes that occurred at the end of the last glaciation in response to rapid warming (18 000–11 000 cal yr BP; [42]).

Evidence of disequilibrium at that time comes from palaeoenvironmental records in both hemispheres. Pollen data from the eastern Patagonian Andes (41–45°S), for example, reveal an early expansion of *Nothofagus* into steppe starting at *ca* 17 000 cal yr BP. Rapid population growth (i.e. net change in population size > 1; equation (2.1)) was associated with migration from glacial refugia and colonization of landscapes previously dominated by grasses. This sustained expansion of trees forced by changes in climate favoured a succession of parklands with no counterparts in the modern vegetation [26,43,44]. After 11 000 cal yr BP, *Nothofagus*-dominated forest developed. Subsequent low climate variability with respect to the tolerances of the ecosystem led to equilibrial communities whose trajectory was mainly driven by site-specific ecological feedbacks.

In the Yellowstone region, a similar period of disequilibrium occurred from 16 000 to 12 000 cal yr BP. As the climate warmed, parkland, initially dominated by *Picea engelmannii*, *Juniperus communis*, *Artemisia* and Poaceae, was replaced by a series of forests that included unusual (by present-day vegetation) mixtures of *Pinus albicaulis*, *Picea* and *Abies* [45]. Disequilibrium is attributed to the rapid rate of warming coupled with slow soil development [46]. The magnitude of the climate change associated with this transition is similar to that projected for the coming decades [20] but future rates of change are orders of magnitude higher, which portends the likelihood of disequilibrial ecosystems and altered disturbance regimes in the years ahead [47].

6. So, if the trees burn, is the forest lost?

The palaeoecological record is fertile ground for understanding forest responses to environmental change. Our examples from the northwestern USA, Patagonia, Tasmania, and New Zealand suggest that the temporal trajectory of temperate forests can be envisioned as partly deterministic (constrained by climate and location), complex (driven by a suite of feedbacks) and stochastic (dependent on legacy effects and disturbance [48]). At the most fundamental level, forest capacity to persist through time is dictated by a location's long-term environmental history and physical site conditions (e.g. geology, topography, climate), which determine the pool of taxa present in the area, their ecological traits, and the emerging biophysical interactions.

During periods of low climate variability, forests tend to recover their structure and function after disturbance through negative, self-regulating feedbacks conducive to stable equilibrium (e.g. *Pinus contorta* and *Nothofagus* forests in Yellowstone and Patagonia, respectively). However, given that the opportunities for recovery to subsequent disturbances are time-dependent, resilience varies as forest composition oscillates around its mean condition. In consequence, regime shifts can be triggered not only by unprecedented events (e.g. anthropogenic burning in New Zealand), but also by disturbance episodes that affect ecosystems approaching a tipping point (e.g. *Nothofagus-Athrotaxis* forests in Tasmania) or catalyse cascading, self-amplifying positive feedbacks that precipitate the transient organization of the system into a structurally and mechanistically different state (e.g. *Pilgerodendron* bog in Patagonia). These case studies show that the emergence of new conditions and altered disturbance regimes can yield profound impacts, even in the absence of climate change.

Vegetation trajectories are highly contextual. Information on the location-specific temporal dimensions of stability, instability and disequilbrium, as well as the conditions that have led to seemingly irreversible regime shifts is fundamental to understanding non-analogue climate scenarios in the future [49,50]. For example, concerns about recent fires and their impact on *Pinus contorta* seed germination in the Yellowstone region [51] can be informed by a comparison with the conditions that led to the dynamic stability of Holocene forests. Similarly, the influence of land-use and large-scale burning on *Nothofagus pumilio* forests in Patagonia and *Lophozonia*-podocarp forests in New Zealand stand in contrast with their relatively stable long-term vegetation-fire dynamics. Palaeoecology thus helps gauge the significance of current changes and target the ecosystem components of greatest vulnerability.

Even if long-term ecosystem dynamics were perfectly known, historically informed efforts will become progressively less relevant as climate and disturbance events exceed the range of observed conditions. Current rates of climate change are already higher than at any time in the Holocene [52], and combined with recent land use, have led to unprecedented changes at some locations, including fragmentation of forests, disruption of biogeochemical cycles, spread of invasive species, and extinction of native fauna and flora [53]. For this reason, forest conservation and management strategies, which are often designed to mitigate native species loss and restore natural disturbance regimes, are revising expectations for the future [54]. The partially stochastic and dynamic nature of ecosystems means that future projections will always be uncertain in both time and space. Interdisciplinary efforts that integrate historical information, experimental testing of theory and process-based modelling are necessary to more accurately estimate uncertainties and assess future ecological scenarios, thus reducing the probability of surprises.

Data accessibility. Pollen and charcoal data are publicly available at Neotoma (www.neotomadb.org) and the Global Charcoal Database (www.paleofire.org), respectively.

Authors' contributions. V.I. and C.W. conceived the study and wrote the manuscript. V.I. carried out the statistical analyses. Both authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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