

## Research



**Cite this article:** Morris JL, DeRose RJ, Brussel T, Brewer S, Brunelle A, Long JN. 2019 Stable or seral? Fire-driven alternative states in aspen forests of western North America. *Biol. Lett.* **15**: 20190011.  
<http://dx.doi.org/10.1098/rsbl.2019.0011>

Received: 7 January 2019  
Accepted: 15 May 2019

**Subject Areas:**  
ecology, plant science

**Keywords:**  
aspen, wildfire, biodiversity, functional diversity, plant traits, resilience

**Author for correspondence:**  
Jesse L. Morris  
e-mail: [jesse.morris@utah.edu](mailto:jesse.morris@utah.edu)

A contribution to the special feature 'Ecological resilience: from theory to empirical observations using long-term datasets' organised by the PAGES EcoRe3 Working Group.

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4514699>.

# Stable or seral? Fire-driven alternative states in aspen forests of western North America

Jesse L. Morris<sup>1</sup>, R. Justin DeRose<sup>2</sup>, Thomas Brussel<sup>1</sup>, Simon Brewer<sup>1</sup>, Andrea Brunelle<sup>1</sup> and James N. Long<sup>3</sup>

<sup>1</sup>Department of Geography, University of Utah, Salt Lake City, UT 84112, USA

<sup>2</sup>Rocky Mountain Research Station, Forest Inventory and Analysis, USDA Forest Service, Ogden, UT 84401, USA

<sup>3</sup>Department of Wildland Resources, Ecology Center, Utah State University, Logan, UT 84322, USA

JLM, 0000-0002-5559-8279

As important centres for biological diversity, aspen forests are essential to the function and aesthetics of montane ecosystems in western North America. Aspen stands are maintained by a nuanced relationship with wildfire, although in recent decades aspen mortality has increased. The need to understand the baseline environmental conditions that favour aspen is clear; however, long-term fire history reconstructions are rare due to the scarcity of natural archives in dry montane settings. Here, we analyse a high-resolution lake sediment record from southwestern, Utah, USA to quantify the compositional and burning conditions that promote stable (or seral) aspen forests. Our results show that aspen presence is negatively correlated with subalpine fir and that severe fires tend to promote persistent and diverse aspen ecosystems over centennial timescales. This information improves our understanding of aspen disturbance ecology and identifies the circumstances where critical transitions in montane forests may occur.

## 1. Introduction

Quaking aspen (*Populus tremuloides*) communities harbour higher levels of plant diversity than associated conifer forests [1], but in recent decades, aspen has experienced widespread decline [2]. Lack of fire disturbances, possibly as a result of fire exclusion programmes, has been implicated as a major driver of aspen loss [3], which may also alter community-level function [4]. To develop aspen restoration strategies, resource managers are interested in understanding the natural dynamics of aspen fire regimes prior to Euro-American settlement. Retrospective studies using tree rings or lake sediments can help reconstruct environmental interactions over long temporal scales [5]. However, two challenges limit fire history reconstructions in aspen. First, moderate- to high-severity burns tend to kill this relatively thin-barked species while also promoting regeneration through clonal reproduction (i.e. 'suckering'). Therefore, tree-ring studies provide few direct measures of fire recurrence and many studies have instead relied on inference from nearby conifer stands [3]. Second, sediment-based reconstructions (i.e. palaeoecological studies) are limited by the rarity of natural lakes in aspen-dominated landscapes. Despite these challenges, recent work showed that aspen increased during a prolonged fire-free period [6], and that drought, accompanied by frequent fire, promoted aspen recruitment [7]. Therefore, a refined understanding of fire's role in maintaining aspen and ecological diversity is possible with further palaeoecological investigation.

Aspen is an ideal ecosystem to test key assumptions and predictions from resilience theory because fire regime shifts tend to promote two alternative

states, i.e. stable or seral [8,9], defined here by relative amounts of aspen and fir and the associated fire regimes. Stable (or seral) aspen systems are maintained by burning, in particular, fire recurrence and severity, which are influenced by fuel structure and fuel moisture. Stable aspen stands are effectively monotypic, mesic and burn infrequently, whereas seral stands experience chronic conifer invasion, largely by subalpine fir (*Abies lasiocarpa*), variable moisture, and frequent, often severe fires because fir commonly acts as a ladder fuel that promotes canopy fires. Assuming timescale-dependence, either status may confer resilience [10]. However, most contemporary forest disturbance literature clearly describes the two states; here we aim to quantify where critical transitions have occurred between stable and seral aspen forests using a lake sediment record.

## 2. Material and methods

Sugarloaf Pond (37°40'20.47", 112°54'13.29", 2886 m) is a small lake (0.27 ha) located in an east-facing cirque in southwestern Utah, USA. Surrounding vegetation is dominated by nearly pure, mature aspen forest approximately 170 years in age. In September 2015, a 2.75 m long sediment core was retrieved in approximately 8 m of water depth at the lake centre. To reconstruct the fire history and past vegetation composition, contiguous sediment subsamples (5 cm<sup>3</sup>) at 1 cm intervals were analysed for charcoal and macrofossils following standard protocols, processed with 125 µm sieves and counted using light microscopy (40×) [11–13]. Conifer needles (i.e. fir) were identified and nine were submitted for radiocarbon (<sup>14</sup>C) analysis to establish age-depth control (electronic supplementary material). Sediment subsamples (1 cm<sup>3</sup>) for pollen were processed, including the introduction of a known quantity of tracers (*Lycopodium*), and counted at 2 cm intervals (i.e. every other cm) using light microscopy (500×) [14].

To reconstruct fire events and recurrence intervals, we converted charcoal counts to concentration (particles/cm) and then charcoal accumulation rates (CHAR, particles cm<sup>-2</sup> yr<sup>-1</sup>). Next, the charcoal concentrations were binned using the median sediment deposition time (10 years) to minimize variations resulting from shifting sedimentation rates. Newly binned concentrations were then converted to CHAR and decomposed into the background (BCHAR) and peak components using CharAnalysis [15]. BCHAR is the slowly varying CHAR trend, and fire peaks are positive deviations from BCHAR, which we interpreted as originating from a fire episode. Peaks were determined using a Lowess smoother, robust to outliers, within a 500 year window [16]. BCHAR values for each time interval were subtracted from total CHAR for each interval. Peaks (i.e. intervals with CHAR values above BCHAR) were tested for significance using a Gaussian distribution, where peaks that exceeded the 95th percentile were considered significant. We applied this procedure for every 500 year overlapping portion of the record, producing a unique threshold for each sample. Lastly, all peaks were screened to eliminate those resulting from statistically insignificant CHAR variations [17]. If the maximum count in a CHAR peak had a greater than 5% chance of coming from the same Poisson-distributed population as the minimum of the preceding 75 years, the peak was rejected [16].

To determine the proportional changes in vegetation composition needed to classify a forest as stable or seral, pollen count data were converted to percentage of the terrestrial sum (electronic supplementary material), and the ratio of aspen to fir pollen was normalized using the formula  $(a - b)/(a + b)$ , where  $a$  = aspen and  $b$  = fir (e.g. [18]). A generalized additive model

(GAM) was used to model trends in the pollen ratio and then used to identify zones of similar vegetation development in the sequence. Following [19], periods of positive or negative trend are inferred as the times when the first derivative of the GAM smoother is significantly different from zero. Each zone in the sequence therefore represents a period of either positive, negative or no trend in the pollen ratio. These zones are then used to highlight critical transitions in the forest community, representing possible tipping points between stable and seral aspen types. Fire events were binned into the same age model as the pollen data, before calculating the absolute change in aspen pollen from before to after each fire event. We used this calculation to measure resilience, specifically recovery (*sensu* [20]), where recovery is indicated by positive values.

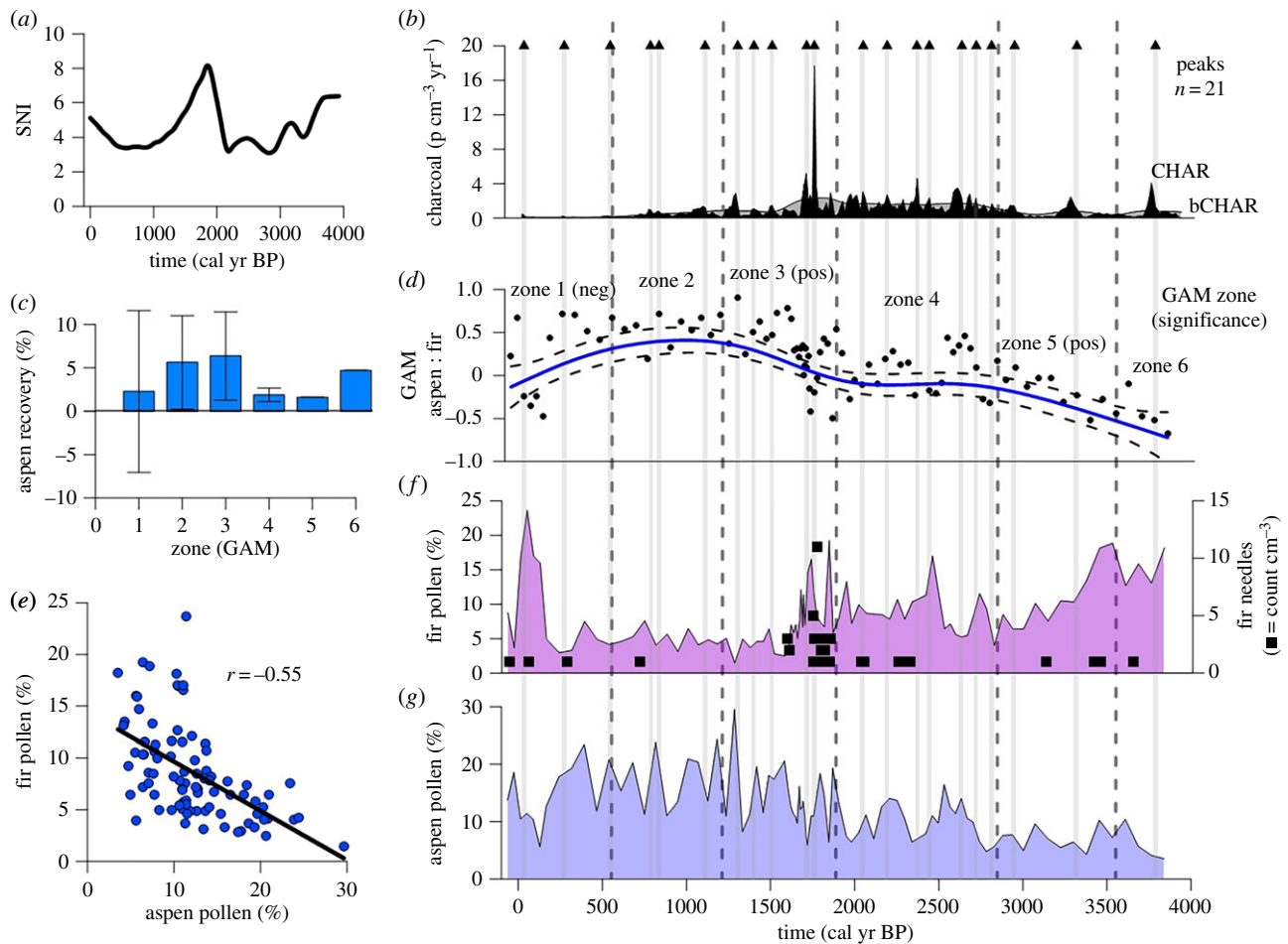
Changes in diversity between seral and stable aspen forests were studied using species evenness and richness, and functional diversity. Evenness was calculated using the slope of the rank-order versus log abundance curve for each sample and richness using rarefaction to a pollen count of 500 grains [21]. Functional diversity was based on three functional traits (seed mass, plant height and leaf area) directly related to plant survival, production and growth [22,23]. Trait data were obtained using the BIEN Database [24] R package [25]. Species-level trait data were processed following [26] and median trait values [27] for each taxon in a given sample were used for hypervolume quantification as a conservative measure of function. Alpha diversity estimations at each pollen sample were quantified using all pollen taxa (site-level: tree and shrub, TRSH; and upland herb, UPHE) and for vegetation types, TRSH and UPHE, separately. Beta overlap is the proportion of shared trait space between hypervolumes of time adjacent samples. Beta estimations were standardized by the elapsed time between pollen samples.

## 3. Results

A signal-to-noise ratio greater than 3 indicated that the charcoal time series was appropriate for peak detection analysis [28] (figure 1*a*). The mean fire-return interval ranged between 150 and 300 years over the last 4000 years, with 21 peaks (table 1 and figure 1*b*). The most prominent event (i.e. highest CHAR) occurred approximately 1700 cal yr BP (1700 fire, hereinafter). Since that time, CHAR and peak episodes are conspicuously lower and less frequent than elsewhere in the record. In the modern watershed, the dominant aspen age was 170 years old, which indicated that a stand-replacing fire has not occurred in at least 170 years.

Over the 4000 year record, fir and aspen pollen were anti-correlated (figure 1*e*), indicating that the presence of one species generally precluded the other. The presence of fir macrofossils was high when fir pollen was high, and vice-versa (figure 1*f*). Changes in the modelled GAM trend identified six periods of distinct vegetation dynamics (table 1 and figure 1*d*).

Prior to the 1700 fire, the diversity indices show low pollen richness coupled with stable functional diversity (figure 2). Evenness declines over this period, indicating that the vegetation was increasingly dominated by a small set of taxa. Samples corresponding to the 1700 fire show a marked impact on the vegetation around the site, with peaks in both richness and evenness, coupled with a large drop in the functional overlap between samples. Diversity indices subsequently return to pre-fire values at around 1500 BP, followed by an increase to maxima by 1000 BP. Richness and functional diversity undergo a slow decline over the last millennium, but evenness remains high, suggesting that



**Figure 1.** Trends in (a) signal-to-noise index (SNI) for charcoal time series; (b) charcoal time series depicting charcoal accumulation rate (CHAR) in black, background charcoal (bCHAR) in grey, and peaks ( $\blacktriangle$ ); (c) histogram showing post-fire recovery for aspen (%) per zone; (d) ratio of aspen to fir (blue line) with a general additive model (GAM) (black line), with Zones 1–6 identified as periods of either significant or non-significant trend (transitions between zones denoted by vertical dashed grey lines); (e) relationship between fir and aspen pollen (%) showing negative correlation (black line); (f) pollen (%) data for fir with fir needle abundances ( $\blacksquare$ ) and (g) pollen (%) data for aspen. (Online version in colour.)

**Table 1.** Summary of vegetation and fire regime dynamics.

zone (GAM)	resilience	standard error (s.e.)	Pearson's $r$ aspen : fir	significance	age (cal year BP)
1	2.29	9.33	-0.66	neg	603
2	5.65	5.40	-0.33	—	1246
3	6.38	5.11	-0.58	pos	1968
4	1.87	0.77	-0.19	—	2944
5	1.60	0.00	0.31	pos	3596
6	4.70	0.00	-0.61	—	—

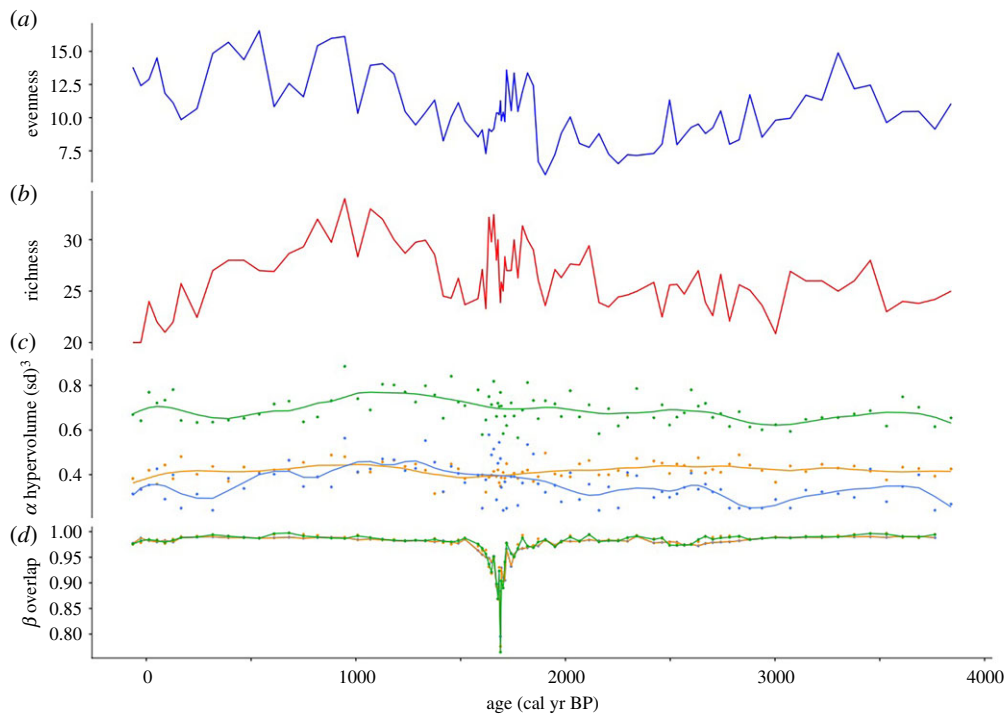
while the vegetation becomes relatively impoverished, no single taxon achieves dominance.

#### 4. Discussion

The pollen and macrofossil records indicated that over the last 4000 years, the forest composition around Sugarloaf Pond alternated between fir and aspen overstory. Despite being characterized as stable or seral, the entire period was characterized by relatively long fire-return intervals that ranged between 150 and 300 years. Diversity metrics provide secondary support for the 'response diversity' [30] of

vegetation to the environmental variation that influences ecosystem resilience. In combination, these lines of evidence suggest that there were at least two distinct 'tipping points' where the Sugarloaf Pond ecosystem transitioned. First, the 1700 fire (Zone 3) caused a switch from seral to stable aspen and subalpine fir was nearly eliminated from the system (Zone 2). The second tipping point is likely taking place over the last two centuries (Zone 1), when fir abundance rebounded, perhaps aided by climate or grazing history, and is likely shifting the system from stable to seral.

Before the 1700 fire, diversity was low but constant (Zones 4–6; seral aspen), when compared to after the fire (Zone 2; stable aspen). Similarly, fir pollen and macrofossils



**Figure 2.** Trends in (a) evenness, (b) richness, (c) alpha diversity and (d) beta overlap. In (c,d), functional site-level diversity and overlap estimates (all terrestrial pollen types, green lines) were decomposed to tree and shrub (TRSH, blue lines) and upland herb (UPHE, orange lines) pollen types. The diversity metrics indicate occupied and shared niche space [29] across pollen assemblage samples. (Online version in colour.)

were abundant prior to the fire when compared to after. Taken together, these lines of evidence indicate a functional shift from seral to stable. Interestingly, aspen recovers quickly which is likely a reflection of functional-disturbance dynamics. We speculate that both seral and stable aspen communities in Zones 2–4 were likely dependent on the occurrence of relatively frequent fires that maintained aspen.

The 1700 fire was a prominent event in this record, which we interpreted as a high-severity fire that burned within (but likely also surrounding) the Sugarloaf Pond catchment. The corresponding rise in CHAR, shift in vegetation GAM and rapid changes in diversity metrics, are all strongly suggestive of a disturbance-mediated ecosystem shift. These data show that the mechanism driving the aspen seral to stable tipping point was fire recurrence, irrespective of subalpine fir presence, and resulted in community-level functional reorganization. In other words, over the long-term, this aspen population tipped from seral to stable, likely driven by the 1700 fire that nearly extirpated fir locally.

The stable aspen-dominated forest established after the 1700 fire remained functionally similar until just recently (Zone 1), where a shift to seral appears to be underway. The increase in alpha diversity after the 1700 fire, alongside elevated levels of aspen pollen, further corroborates the case for a long-term stable aspen community, maintained by the relatively frequent fire regime. We contend that previous (and subsequent) burns were not as high severity as the 1700 fire. For instance, minor decreases in functional similarity in seral vegetation at approximately 2700 cal yr BP (Zone 4) were associated with fire events. The absence of a strong response in functional and alpha diversity suggests that the approximately 2700 cal yr BP and other burning events were of lower severity compared with the 1700 fire. However, the decline in richness and functional diversity towards present reflects the recent influx of subalpine fir

pollen, suggesting that this system is potentially shifting from stable to seral.

More importantly, in combination with the increasing presence of subalpine fir, the recurrence of the fire has lengthened, which in unison has not promoted aspen. As a result, the shift from Zone 2 to Zone 1 likely indicates a transition from aspen stability to emerging aspen sensitivity. Zone 1 had substantial recent subalpine fir establishment, the result of an ageing stable aspen stand (approx. 170 years old) and few fires. The absence of recent fires was partly due to reduction in fuels from intense pastoralism (circa 1880s) [31]. However, the decline in aspen pollen began before this era, which suggests that other factors may also be influencing fire–vegetation dynamics. Climate is a likely possibility, and subtle shifts from dry to more mesic conditions over the past two centuries indicated in tree-ring studies from this region [32] may have been favourable for drought-sensitive fir (relative to aspen) recruitment around Sugarloaf Pond. However, from a broader perspective, the decreasing richness concomitant with relatively stable evenness over the last millennium suggests that while climate may be shifting, its effects may be subtle.

We found shifting ecosystem resilience was the result of a dynamic interplay between fire events and forest overstory composition. Forest succession in this aspen community was characterized by two key tipping points over the last 4000 years, where it transitioned from seral to stable, mediated by high-severity fire, and likely back to seral in recent centuries. Irrespective of shifting subalpine fir abundance, recurrent fire maintained aspen until recently, where infrequent fire coupled with increasing subalpine fir—likely from climate and/or human activities—threatens the persistence of the aspen community surrounding Sugarloaf Pond. Future work is needed to further assess resilience in montane aspen systems and specifically the roles imposed by climate

and human activities. Palaeoecological approaches, such as those reported here, may benefit in the future from more spatio-temporally resolved 'neocological' methods of understanding the dynamics of seral and stable aspen across landscapes [33].

**Data accessibility.** The datasets supporting this article have been uploaded as part of the electronic supplementary material.

**Authors' contributions.** J.L.M. and R.J.D. conceived the study; J.L.M. conducted the laboratory experiments; J.L.M., R.J.D., T.B., J.L., S.B. and A.B. analysed the data; J.L.M., R.J.D., T.B., S.B., A.B. and J.L. wrote

the manuscript. All authors approved the final version and agree to be held accountable for the content therein.

**Competing interests.** We declare that we have no competing interests.

**Funding.** This work was supported by State of Utah, Cedar Mountain Initiative.

**Acknowledgements.** We thank the Center for Applied Isotope Studies at the University of Georgia for radiocarbon analysis, Stacy Morris for laboratory work and John Israelsen and Dan Mckenna for assistance with fieldwork. This paper was prepared in part by an employee of the US Forest Service as part of official duties and is therefore in the public domain.

## References

- Kuhn TJ, Safford HD, Jones BE, Tate KW. 2011 Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape. *Plant Ecol.* **212**, 1451. (doi:10.1007/s11258-011-9920-4)
- Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B. 2010 Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *For. Ecol. Man.* **26**, 638–648. (doi:10.1016/j.foreco.2010.05.020)
- Shinneman DJ, Baker WL, Rogers PC, Kulakowski D. 2013 Fire regimes of quaking aspen in the Mountain West. *For. Ecol. Man.* **299**, 22–34. (doi:10.1016/j.foreco.2012.11.032)
- Brussel T, Minckley TA, Brewer SC, Long CJ. 2018 Community-level functional interactions with fire track long-term structural development and fire adaptation. *J. Veg. Sci.* **29**, 450–458. (doi:10.1111/jvs.12654)
- Dearing JA, Braimoh AK, Reenberg A, Turner BL, Van der Leeuw S. 2010 Complex land systems: the need for long time perspectives to assess their future. *Ecol. Soc.* **15**, 21. (doi:10.5751/ES-03645-150421)
- Morris JL, Brunelle A, Munson AS, Spencer J, Power MJ. 2013 Holocene vegetation and fire reconstructions from the Aquarius Plateau, Utah, USA. *Quat. Intl.* **310**, 111–123. (doi:10.1016/j.quaint.2012.10.055)
- Carter VA, Brunelle A, Minckley TA, Shaw JD, DeRose RJ, Brewer S. 2017 Climate variability and fire effects on quaking aspen in the central Rocky Mountains, USA. *J. Biog.* **44**, 1280–1293. (doi:10.1111/jbi.12932)
- Scheffer M *et al.* 2012 Anticipating critical transitions. *Science* **338**, 344–348. (doi:10.1126/science.1225244)
- Rogers PC, Landhäusser SM, Pinno BD, Ryel RJ. 2014 A functional framework for improved management of Western North American aspen (*Populus tremuloides* Michx.). *For. Sci.* **60**, 345–359. (doi:10.5849/forsci.12-156)
- Davies AL, Streeter R, Lawson IT, Roucoux KH, Hiles W. 2018 The application of resilience concepts in palaeoecology. *Holocene* **28**, 1523–1534. (doi:10.1177/0959683618777077)
- Clark JS. 1988 Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quat. Res.* **30**, 67–80. (doi:10.1016/0033-5894(88)90088-9)
- Whitlock C, Millsaugh SH. 1996 Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *Holocene* **6**, 7–15. (doi:10.1177/095968369600600102)
- Gardner JJ, Whitlock C. 2001 Charcoal accumulation following a recent fire in the Cascade Range, northwestern USA, and its relevance for fire-history studies. *Holocene* **11**, 541–549. (doi:10.1191/095968301680223495)
- Faegri K, Iversen J. 1989 *Textbook of pollen analysis*. Chichester, UK: John Wiley and Sons.
- Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA. 2009 Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecol. Mono.* **79**, 201–219. (doi:10.1890/07-2019.1)
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ. 2010 Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int. J. Wildl. Fire* **19**, 996–1014. (doi:10.1071/WF09134)
- Gavin DG, Hu FS, Lertzman K, Corbett P. 2006 Weak climatic control of stand-scale fire history during the late Holocene. *Ecology* **87**, 1722–1732. (doi:10.1890/0012-9658(2006)87[1722:WCCOSF]2.0.CO;2)
- Mensing S, Smith J, Norman KB, Allan M. 2008 Extended drought in the Great Basin of western North America in the last two millennia reconstructed from pollen records. *Quat. Int.* **188**, 79–89. (doi:10.1016/j.quaint.2007.06.009)
- Simpson GL. 2018 Modelling palaeoecological time series using generalized additive models. *Front. Ecol. Evol.* **6**, 149. (doi:10.3389/fevo.2018.00149)
- Hodgson D, McDonald JL, Hosken DJ. 2015 What do you mean, 'resilient'? *Trends Ecol. Evol.* **30**, 503–506. (doi:10.1016/j.tree.2015.06.010)
- Giesecke T, Ammann B, Brande A. 2014 Palynological richness and evenness: insights from the taxa accumulation curve. *Veg. Hist. Archaeobot.* **23**, 217–228. (doi:10.1007/s00334-014-0435-5)
- USDA, NRCS. 2018 *The PLANTS database* (<http://plants.usda.gov>, 14 November 2018). Greensboro, NC: National Plant Data Team.
- Díaz S *et al.* 2016 The global spectrum of plant form and function. *Nature* **529**, 167. (doi:10.1038/nature16489)
- Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers BM. 2009 The Botanical Information and Ecology Network (BIEN): cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. See [http://www.iplantcollaborative.org/sites/default/files/BIEN\\_White\\_Paper.pdf](http://www.iplantcollaborative.org/sites/default/files/BIEN_White_Paper.pdf).
- Maitner BS *et al.* 2018 The BIEN R package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Meth. Ecol. Evol.* **9**, 373–379. (doi:10.1111/2041-210X.12861)
- Blonder B, Lamanna C, Violle C, Enquist BJ. 2014 The n-dimensional hypervolume. *Glob. Ecol. Biog.* **23**, 595–609. (doi:10.1111/geb.12146)
- Reitalu T, Gerhold P, Poska A, Pärtel M, Väli V, Veski S. 2015 Novel insights into post-glacial vegetation change: functional and phylogenetic diversity in pollen records. *J. Veg. Sci.* **26**, 911–922. (doi:10.1111/jvs.12300)
- Kelly RF, Higuera PE, Barrett CM, Hu FS. 2011 A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quat. Res.* **75**, 11–17. (doi:10.1016/j.yqres.2010.07.011)
- Whittaker RH. 1972 Evolution and measurement of species diversity. *Taxon* **21**, 213–251. (doi:10.2307/1218190)
- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J. 2003 Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494. (doi:10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2)
- Hall M. 2001. Repairing mountains: restoration, ecology, and wilderness in twentieth-century Utah. *Environ. Hist.* **6**, 584–610. (doi:10.2307/3985256)
- Salzer MW, Kipfmüller KF. 2005 Reconstructed temperature and precipitation on a millennial timescale from tree-rings in the southern Colorado Plateau, USA. *Clim. Change* **70**, 465–487. (doi:10.1007/s10584-005-5922-3)
- Buma B *et al.* 2019 The value of linking paleoecological and neocological perspectives to understand spatially-explicit ecosystem resilience. *Land. Ecol.* **34**, 17–33. (doi:10.1007/s10980-018-0754-5)