**Monitoring British Upland Ecosystems Using Landscape Structure as an Indicator for State-and-Transition Models.**

*Dylan Young1, Humberto L. Perotto-Baldivieso2, Tim Brewer3, Rachel Homer4, Sandra A. Santos5*

**\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_**

*Authors are 1 Research Postgraduate, School of Geography, University of Leeds, Leeds, LS2 9JT, UK; 2 Lecturer, 3 Senior Lecturer, Department of Environmental Science and Technology, Cranfield University, Cranfield MK43 0AL, UK; 4Statistics and Numeracy Support Assistant, School of Geography, University of Leeds, Leeds, LS2 9JT, UK; 5 Researcher, Embrapa Pantanal, EMBRAPA, Corumbá, Brazil.*

Research was supported by the North Lakes National Trust, the National Trust and Natural England.

At the time of the research, Young was an MSc student and Santos was a visiting researcher, Department of Environmental Science and Technology, Cranfield University, Cranfield MK43 0AL, United Kingdom.

Correspondence: Humberto L. Perotto-Baldivieso, Department of Environmental Science and Technology, Building 42, Cranfield University, Cranfield, MK43 0AL, United Kingdom. Email: h.perotto@cranfield.ac.uk

Current address: Dylan Young, School of Geography, University of Leeds, University Road, Leeds, LS2 9JT, UK; Sandra A. Santos, Embrapa Pantanal, Caixa Postal 109 - Corumbá, MS- Brasil - 79320-900.

ABSTRACT

Remote sensing and landscape ecology concepts can provide a useful framework for state-and-transition models (STM) in order to quantify thresholds at different scales, and provide useful information for scientists, land managers and conservationists in relation to resilience management. The overall aim of this research was to develop a spatially explicit STM to quantify thresholds based on the scale of disturbance processes impacting a grazing system. Specific objectives were to develop a conceptual STM framework for upland grazing ecosystems, to quantify spatial dynamics of stable and degraded pastures, and to assess threshold occurrence. Color aerial photography from Armboth Fell in the English Lake District National Park (United Kingdom) was classified into bare rock, dwarf shrub heath (DSH), and grassland/degraded wet heath (GDWH) in four pastures with different degrees of grazing pressure. Vegetation communities from these pastures were combined with soils, climate and landform data to create a conceptual STM framework. Each pasture was sampled with 2 ha plots to quantify DSH and GDWH spatial structure. The proposed STM consisted of two reference and three alternative states. Low grazing pressure areas showed significantly higher percentage of DSH cover with larger contiguous patches and lower patch density than high grazing pressure areas. Breakpoints, considered to be thresholds, in mean patch area were identified in our data when DSH percentage cover was < 63% and GDWH, > 77%. The present study has shown the value of a robust, reliable, and repeatable approach to identify landscape dynamics and integrate it with field data to inform a conceptual STM framework for upland grazing ecosystems. It also demonstrates the importance of selecting scales relevant to the predominant disturbance process to test for threshold occurrence, and how this approach can be integrated with current assessment methods for resilience management.

**Key Words:** grazing, landscape ecology, peatland, remote sensing, resilience, thresholds

INTRODUCTION

State-and-transition models (STM) have been widely used in rangelands as an alternative to the equilibrium succession paradigm in order to improve our understanding of vegetation dynamics and in, particular, the concepts of resilience and thresholds (Westoby et al. 1989). STMs have been developed and used in rangelands for a number of years mostly in arid and semi-arid ecosystems to evaluate alternative management scenarios (e.g. Australia [Ash et al. 1994]) and to design control approaches for encroaching shrubs (e.g. North America [Steele et al. 2012; Bestelmeyer et al. 2013]). The use of STMs has been expanded to include other ecosystems such as an Australian woodland habitat, demonstrating scope for use beyond the original application (Rumpff et al. 2011). Although STMs have been criticised for remaining conceptual and qualitative (Sadler et al. 2010; Rumpff et al. 2011), recent work has focussed on adding quantitative analyses including a greater emphasis on heterogeneity and spatial and temporal patterns for threshold identification (Bestelmeyer et al. 2011, 2013; Steele et al. 2012; Twidwell et al. 2013). Ecological thresholds are an important concept for conservation management and in conjunction with STMs can be used to describe the triggers that lead to changes to alternative and often undesired vegetation communities (Briske et al. 2006). Reversal of these changes can be difficult due to the presence of hysteresis which can result in continued landscape degradation even when disturbance pressure is reduced (e.g. reduction in grazing) (Scheffer et al. 2001). Triggers that cause these changes can be related to autogenic processes such as succession, or allogenic factors such as inappropriate land management, climatic events or a combination of both. Thresholds represent a spatiotemporal point or range of decreased ecological resilience beyond which the potential for autogenic repair is lost (Stringham et al. 2003; Betts et al. 2007), which requires management intervention to return a site to a state of pre-threshold conditions (Westoby et al. 1989; Bestelmeyer 2006; Sadler et al. 2010). Although such points of discontinuous change do not exist in all habitats (Suding and Hobbs 2009), an ability to identify and monitor conditions that could lead to a shift in states can provide land managers, ecologists and researchers with the information needed to: (i) avoid crossing thresholds by developing an understanding of ‘at risk’ (least resilient) vegetation phases (Briske et al. 2008); (ii) identify habitats where autogenic recovery is unlikely and; (iii) identify where restoration efforts are likely to be most effective. Considering that the cost in both time and money of post-threshold restoration pathways (if viable) is likely to be greater than that of pre-threshold habitats, the identification of thresholds and related indicators for use in monitoring of important habitats should be of high priority.

The scale of disturbance processes is highly relevant when identifying thresholds, and therefore, spatially explicit approaches may be useful when aiming to identify both drivers and indicators of landscape change (Williamson et al. 2012). Landscape ecology concepts such as the relationship between pattern and process can provide a useful framework to quantify thresholds at different scales and provide information that facilitates decision-making for scientists, land managers and conservationists (Arancibia Arce et al. 2013). In addition, the use of geographic information systems (GIS) and remote sensing based methodologies can provide a useful link to incorporate these quantitative approaches into the STM framework (Bestelmeyer et al. 2011). A number of studies have also used remote sensing in conjunction with STMs, but few have used spatially explicit models to quantify structural thresholds based on the scale of the prevailing disturbance processes (e.g. grazing). Sadler et al. (2010) used close range photogrammetry to develop an STM-based on an ordination of image metrics and Steele et al. (2012) used aerial image interpretation to classify and map ecological states.

An STM framework has not yet been developed for grazing on UK moorland and blanket bog communities. Blanket bog is a carbon-rich high-latitude ombrotrophic peatland which along with other peat ecosystems have become of great interest with regards to the feedbacks that may be exerted on the climate system through carbon dioxide and methane fluxes (Charman et al. 2012). Thompson et al. (1995) described changes due to anthropogenic pressures on the succession of *Calluna vulgaris* (L.) Hull dominated moorland and blanket bog communities in an STM-like diagram, but did not differentiate between possible alternative ecosystem states and within-state transitions (community phases) or attempt to quantify thresholds. Therefore, the aim of this research was to develop an STM with a spatially explicit component to quantify thresholds based on the scale of disturbance processes. The specific objectives were; 1) to develop a conceptual STM framework for upland grazing ecosystems; 2) quantify spatial dynamics of stable and degraded pastures and; 3) estimate thresholds between states. To achieve these aims and objectives we combined remote sensing techniques, STM principles and landscape ecology metrics using, as a case study, an upland ecosystem in the United Kingdom (UK), with the potential to be used in similar areas worldwide. These ecosystems encompass habitats of high conservation value whilst providing important ecosystem services such as regulating carbon storage and water quality as well as supporting local livelihoods such as upland sheep farming and game-keeping (Reed et al. 2009; UK NEA 2011; Bellamy et al. 2012). Blanket bogs in the United Kingdom account for approximately 15% of worldwide blanket bog habitats, and mountains, moorlands and heaths hold approximately 40% of British soil carbon in peat and peaty soils and provide 70% of drinking water (Holden 2005, UK NEA 2011).

METHODS

**Study Area**

Our study area was located on Armboth Fell Site of Special Scientific Interest (SSSI) in the English Lake District Special Area of Conservation (54o32’3”N, 3o6’24”W) (Fig. 1). Topography is plateau-like with a high point of 608 m which combined with a cool and wet climate has encouraged the development of blanket bog on flatter areas with shallow peat on gentle slopes and stony loam on steep valley sides (NSRI 2011a). Mean annual rainfall is approximately 1 500 mm, the majority falling between October and February (Met Office 2011). Vegetation cover, based on the British National Vegetation Classification (NVC) (Rodwell 1991), consists mainly of nationally important blanket bog mosaic (Lake District Special Planning Board 1986), wet heath *Tricophorum cespitosum* (L.) Hartm - *Erica tetralix* L. (NVC M15) and dry heath *C. vulgaris* - *Vaccinium myrtillus* L. (NVC H12) with degraded areas of acid grasslands *Juncus squarrosus* L. - *Festuca ovina* L. (NVC U6) and *Nardus stricta* L. - *Galium saxatile* L. (NVC U5) communities. Armboth Fell has been the subject of intensive management for a number of decades with visible signs of grazing, trampling and burning that has resulted in some dry heath, wet heath and blanket bog communities in poor or unfavourable condition (Jerram 2005).

**Data Collection**

Color aerial photography from 2001 of Armboth Fell (0.28 m resolution) was provided by the National Trust that encompassed four land units (G1, G2, G3 and G4) with different grazing regimes. Grazing intensity was variable across sites (G1, 0.74 ewes [*Ovis aries* L.] • ha-1; G2, and G3, 0.66 ewes • ha-1; G4, 1.04 ewes • ha-1) and years depending on stewardship schemes which govern land management practices. The study area was not subject to irrigation or additional inputs such as manure, lime, herbicides, supplemental feeding and no burning has been conducted in since 2005. Condition assessment data produced by Natural England was acquired along with upland vegetation guides (Rodwell 1991; Averis et al. 2004; JNCC 2009) to gather evidence of persistent alternative states. A digital elevation model (DEM) (Ordnance Survey 2011), soil report and associated database (NSRI 2011a, b) and rainfall data for the nearest weather station (Keswick, UK, ≈ 4 km from study site) (Met Office 2011) were acquired to inform the development of the STM.

**Data Analysis**

To develop the STM framework, nine vegetation communities based on NVC descriptions (Rodwell 1991) and 21 community transitions were identified for the study area and grouped into proposed states and transitions (Table 1). These were combined with soils, climate and landform data, discussed with local and national experts and validated with ground observations to form the basis of the conceptual STM. Data in Table 1 was reviewed for suitability for image classification purposes in order to introduce empirical data from the study site to the conceptual STM framework. Gradients were added for water, soil, topography and management treatment so that each state could be placed in a landscape context for the identification of spatial structures that could be measured using metrics derived from remotely sensed data (Banks-Leite et al. 2011). Ground-based assessment revealed the dominant dwarf shrub species to be *Calluna vulgaris*, a significant component of the main classes of vegetation communities on Armboth Fell, which proposed as a suitable indicator for subsequent spatial structure analysis because of patch fragmentation caused by grazing (Palmer and Hester 2000).

The color aerial photographs of 0.28 m resolution were resampled to 2.8 m to reduce spectral variability (Meddens et al. 2011). Red and green bands were used to create a pseudo-normalized difference vegetation index (P-NDVI). The P-NDVI layer was combined with the remaining original bands and classified into three classes (bare rock, dwarf shrub heath [DSH], and grassland/degraded wet heath [GDWH]) using an unsupervised classification in ERDAS Imagine (Intergraph) (Perotto-Baldivieso et al. 2009). Gramminoids and wet heath were combined in our final classification scheme due to difficulties in accurately classifying them separately. Overall accuracy was assessed by using a confusion matrix (Congalton 1991) with 800 randomly sampled points over the whole study area. Classification accuracy was 79.9% ± 1.7 SE. Classified images were used to assess the amount and spatial distribution of DSH and GDWH in each land unit by using the minimum stocking rate suggested to initiate removal of *C.vulgaris* (0.5 ewes • ha-1) (Averis et al. 2004). Although stocking rates in the study area were higher (> 0.6 ewes • ha-1) than the minimum proposed by Averis et al. (2004), the latter was used as a potential threshold that could initiate vegetation degradation in these ecosystems. Sampled areas (2 ha) were randomly generated within each land unit following a similar methodology to Perotto-Baldivieso et al. (2009). Metrics that provide information about the distribution and spatial structure were quantified for each sampled area; percentage landscape (PLAND; %), mean patch area (MPA; ha), patch density (PD; patches • ha-1), largest patch index (LPI; ha) and edge density (ED; m • (100 ha)-1) (Perotto-Baldivieso et al. 2009, 2011). Landscape metrics were compared between land units for significant differences using Kruskal-Wallis one-way variance (p < 0.05) due to unequal variances and non-normal distributions (Dickins et al. 2013). The two classes that provided most information about the state of the pasture, DSH and GDWH, were assessed to identify the occurrence of thresholds using the segmented package in R (Muggeo 2003, 2008; Betts et al. 2007; R Core Team 2013). An estimate of breakpoints was established by testing for a change in slope using the Davies test. This estimated value was then used in the piecewise regression function of the segmented package to test for breakpoints in MPA as a function of PLAND. Values of MPA were selected for analysis as sheep grazing drives fragmentation by significantly reducing the area of *C. Vulgaris* patches (Hester and Baillie 1998; Palmer and Hester 2000). Results from the conceptual STM, landscape metrics and statistical tests were interpreted to propose an STM for an upland grazing ecosystem.

RESULTS

The conceptual STM consisted of five states: two reference states and three alternative states (Fig. 2). These were 1) blanket bog mosaic; 2) dry heath mosaic; 3) wet heath; 4) wet grassland and 5) acid grassland (Table 1). Wet grassland was classified as a transitional state because without grazing it is thought that heath rush(*Juncus squarrosus*) - sheeps fescue (*Festuca ovina*) are likely to ultimately return to wet heath or blanket bog (Averis et al. 2004)*.* Wet heath and acid grassland states (*Nardus stricta* - *Galium saxatile*) were classified as threshold states (Table 1). Transitions were identified between blanket bog mosaic (state I) and wet heath (state II); blanket bog mosaic and acid grassland (state V); dwarf shrub dry heath mosaic (state III) and acid grassland (Fig. 2). Reversible transitions were identified between; blanket bog mosaic and wet grassland (state IV); wet heath and wet grassland; and, dwarf shrub dry heath mosaic and wet grassland.

#### The overall amount of DSH cover was significantly higher in G1 (72.0%); than G2 (44.3%), G3 (20.2%) and; G4 (15.2%) (χ2 = 12.22; df = 3; *P* < 0.01) (Fig. 3a). Similarly, significantly higher values for MPA (0.2 ha; χ2 = 13.3; df = 3, *P* < 0.01) and LPI (14.93 ha; χ2 = 14.05; df = 3; *P* < 0.01) were observed in G1 (Figs. 3c and 3e respectively). Values of PD were highest in G4 (2 779.58 patches • ha-1) as a result of high levels of fragmentation and a reduction in heather patch dominance, and there were significant differences with the other land units (Fig. 3e). Conversely, mean values for PD in G1 (536.65 patches • ha-1) and G2 (1043.48 patches • ha-1) were the lowest (χ2 = 11.97; df = 3; *P* < 0.01) indicating that larger more contiguous patches of DSH (Fig. 3i) occupy these land units. No significant differences were observed for ED (χ2 = 4.19; df = 3; *P* = 0.242) between any of the land units (Fig. 3g). Grassland metrics demonstrated the opposite trend for each land unit because the quantity of bare rock in the classification scheme was small (3.1%). Fragmentation of *C. vulgaris* due to prolonged grazing pressure resulted in an increase in gramminoids (G1, 24.78%; G2, 53.69%; G3, 76.2% and; G4 81.17%) that had invaded the heather patch boundary (Fig. 3b, 3h). As a result, MPA (Fig. 3d) decreased significantly across the four land units (*P* < 0.001) with *C. vulgaris* being confined to smaller less well connected and more compact patches as grazing intensity increased. We found a nonlinear relationship between MPA and PLAND as a result of increased grazing (Fig. 4). Significant changes in slope were observed when PLAND = 63.88% (*P* < 0.0001) in DSH and PLAND = 74.31 (*P* < 0.0001) in GDWH (Fig 4). Breakpoints were found in both DSH and GDWH classes where values for PLAND were 63.16% + 2.85 SE (*r²* = 0.908; *P* < 0.0001) and 77.53% + 2.53 SE (*r²* = 0.79; *P* < 0.0001) respectively.

DISCUSSION

Spatially-explicit data based on landscape structure contributes significantly to model development and threshold identification within an STM framework. Our study has shown the value of combining empirical data derived from remote sensing and landscape metrics with a conceptual STM for resilience-based ecosystem management. Our research specifically sought to combine expert-based knowledge of upland grazing ecosystems with landscape structure-based analysis of relevant spatial disturbance scales, in this case grazing, to identify structural thresholds associated with the states identified in our STM framework. It has been widely proposed that the inclusion of quantitative data can improve the usefulness of STMs to understand the prevailing ecological processes that affect resilience (Sadler et al. 2010; Bagchi et al. 2013; Bestelmeyer et al. 2013) and, as far as we are aware, this study is the first to apply an STM-based approach to a UK upland grazing ecosystem and to a blanket bog. Habitat assessments in upland grazing ecosystems are carried out by field-experts who judge condition by taking account of target species presence and structure and can include visual examination of aerial images to estimate vegetation extent (e.g. JNCC 2009). However, estimates of vegetation cover alone may not be reliable and it is difficult to take into account non-linearities in patch dynamics, such as the relationship we found in landscape structure. Our approach builds a link between landscape ecology and ground-based surveys to more accurately assess the magnitude and direction of change and improve habitat management decision-making. Integrating within- patch vegetation composition, soil properties, ground-based vegetation assessment and the proposed STM could significantly contribute to the development of within-state community phase dynamics.

Alternative states based on a literature review were hypothesised because many UK upland habitats have been grazed or drained or burned (or combinations of) as part of land management systems which can result in upland vegetation communities that tend to be dominated by gramminoids and ericaceae (Yallop et al. 2006; Wilson et al. 2011). Although burning and draining are not part of current management practices both prescriptions have been carried out in the past. The vegetation communities in our study area had been subjected variable grazing pressures (ranging from 0.66 ewes • ha-1 to 1.04 ewes • ha-1) with higher stocking rates than recommended to minimize vegetation degradation and as a result of such continuous disturbance some areas were considered to be in unfavourable condition (Jerram 2005). Such disturbances can lead to discontinuities and in the case of draining (which was often coupled with grazing), produce altered hydrological properties with the result that it may be difficult, even with management intervention, to return to previous states of ecological function (Holden 2005; Wallage and Holden 2011; Bellamy et al. 2012). In addition, there is evidence that a number of the processes within some peatlands are nonlinear and can result in alternative states because of cross-scale feedbacks and self-organisation of vegetation communities (Lamers et al. 2000; Belyea 2009; Eppinga et al. 2009). Patterning has been proposed as an indicator of transition between states comprised of more homogenous vegetation configurations in a number of landscapes including peatlands (Eppinga et al. 2009). This appears to be the case on Armboth Fell where breakpoints in our data separate land units according to mean patch area (Fig. 4). Neither homogeneous DSH nor GDWH configurations seem desirable as such anthropogenic systems may be more likely to collapse when perturbed because they lack the diversity to maintain resilience (MacDougall et al. 2013). The identified structural thresholds based on a significant change of slope and breakpoints in the mean patch area of an indicator species provide the opportunity to add resilience management to current landscape assessment approaches. However, as there is no evidence of hysteresis, it may be most suitable to interpret the identified thresholds as regions of rapidly decreasing resilience as suggested by Betts et al. (2007). Quantifying the resilience of ecosystems and associated thresholds is known to be difficult, and there are doubts over the real-time use of measures of resilience for management purposes (Boettiger and Hastings 2012; Dakos and Hastings 2013). Others have suggested indicators derived from spatial data such as remotely sensed images as one possible way forward because of the paucity of long time series for ecological systems (Carpenter 2013). Our study provides a framework where remotely sensed images can be used to quantify landscape structure and hence identify potential breakpoints which we have interpreted as reduced resilience. This information, integrated with ground-based fieldwork methodologies and multi-temporal image analysis, could significantly improve the information relayed to scientists and land managers. This approach would then become part of a continuous development cycle to improve both the STM and ground-based assessment processes.

Remote sensing techniques can provide fast, accurate and cost effective assessments over large areas to support the STM framework. Data such as ours is more readily and easily obtained at multiple scales and resolutions than long time series (Carpenter 2013) and is well suited to STM development. The analysis of aerial photography was used to quantify spatial structure in relation to sheep grazing which is the predominant disturbance processes. Remote sensing approaches have several advantages over traditional ground-based descriptive methods including accuracy, cost and repeatability. A classification accuracy of 79.9% was achieved using an unsupervised classifier which is comparable to other studies, although alternative approaches could be tested and combined with multi- or hyperspectral images to further improve accuracy (Bradter et al. 2011; Lucas et al. 2011). In addition, remote sensing approaches, combined with ground observations, offer advantages over traditional fieldwork assessments which tend to be hard to repeat over large areas due to between-assessor errors and the significant investment in time and logistics needed (Cherril and McClean 1995; Watson and Novelly 2004; Bastin and Ludwig 2006; Sadler et al. 2010; Bradter et al. 2011). Although multi-temporal images were not available in our study, future assessments using a similar methodology could be replicated to assess both spatial and temporal changes. Greatest benefit would be realised by combining approaches and as such these assessments should also be brought together with field-based validation and expert opinion to establish a robust STM framework for upland grazing ecosystems.

IMPLICATIONS

A combination of expert opinion, remote sensing data and vegetation structure analysis provided a robust approach for quantification of thresholds, and to develop a conceptual STM for our study area. The choice of scale (in our case. 0.5 ewe • ha-1) relevant to the disturbance process was important for the identification of breakpoints in the spatial structure of our chosen indicator species which we interpreted as thresholds in the STM framework. The inclusion of relevant spatial structures may improve our understanding of the direction and magnitude of change as well as the accuracy, reliability and repeatability of the assessment process and can complement current fieldwork methods. The proposed approach uses cost-effective and repeatable methodologies over large areas that could be used to incorporate a multi-temporal analysis not only in upland grazing ecosystems but in any landscape where STM frameworks are applicable. Our findings suggest that these methodologies could be used as part of future resilience-based assessments when developing STMs.

ACKNOWLEDGMENTS

We would like to thank Penny Webb and Alistair Starling and their team at the North Lake District National Trust, John Hoosan of the National Trust and Jean Johnston of Natural England for their support whilst conducting this research. We are very grateful to Helen Armstrong (Broomhill Ecology), John Ludwig (formerly of CSIRO) and the people who provided expert advice on grazing systems and for the development of the STM and to the two anonymous reviewers who helped to significantly improve this manuscript.

LITERATURE CITED

Ash A.J., J. A. Bellamy and T. G. H. Stockwell. 1994. State and transition models for rangelands. 4. Application of state and transition models to rangelands in northern Australia. *Tropical Grasslands* 28: 223–228.

Arancibia Arce, L. R., H. L. Perotto-Baldivieso, J. R. Furlán, M. Castillo-García, L. Soria, and K. Rivero Guzmán. 2013. Spatial and temporal assessment of fragmentation and connectivity analysis for ecotourism activities in a RAMSAR site: Bañados de Isoso (Santa Cruz, Bolivia). *Ecología en Bolivia* 48: 87–103. (In Spanish)

Averis, A. B. G., A. M. Averis, H. J. B. Birks, D. Horsfield, D. B. A.Thompson, and M. Yeo. 2004. An illustrated guide to British upland vegetation. Cambridge, United Kingdom: Joint Nature Conservation Committee. 454 p.

Bagchi, S., D. D. Briske, B. T. Bestelmeyer, and X. B. Wu. 2013. Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. *Journal of Applied Ecology* 50: 1131–1141.

Banks-Leite, C., R. M. Ewers, V. Kapos, A. C. Martensen, and J. P. Metzger. 2011. Comparing species and measures of landscape structure as indicators of conservation importance. *Journal of Applied Ecology* 48: 706–714.

Bastin, G. N. and J. A. Ludwig. 2006. Problems and prospects for mapping vegetation condition in Australia's arid rangelands. *Ecological Management and Restoration* 7: 71–74.

Bellamy, P. E., L. Stephen, I. S. Maclean, and M. C. Grant. 2012. Response of blanket bog vegetation to drain-blocking. *Applied Vegetation Science* 15: 129–135.

Belyea, L. R. 2009. Nonlinear dynamics of peatlands and potential feedbacks on the climate system. *In:* Baird, A. J., L. R. Belyea, X. Comas, A. Reeve, and L. Slater [eds.]. Carbon Cycling in Northern Peatlands, Geophysical Monograph Series 184. Wasington D.C., USA: American Geophysical Union. p. 5–18.

Bestelmeyer, B. T. 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology* 14: 325–329.

Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial perspectives in state-and-transition models: A missing link to land management? *Journal of Applied Ecology* 48: 746–757.

Bestelmeyer B. T., M. C. Duniway, D. K. James, L. M. Burkett and K. M. Havstad. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecology Letters* 16: 339–345.

Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* 21: 1046–1058.

Boettiger, C., and A. Hastings. 2012. Early warning signals and the prosecutor's fallacy. *Proceedings of the Royal Society B: Biological Sciences* 279: 4734–4739.

Bradter, U., T. J. Thom, J. D. Altringham, W. E. Kunin, and T. G. Benton. 2011. Prediction of National Vegetation Classification communities in the British uplands using environmental data at multiple spatial scales, aerial images and the classifier random forest. *Journal of Applied Ecology* 48: 1057 –1065.

Briske, D. D., S. D. Fulhendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management* 59: 225–236.

Briske, D. D., B. T. Bestelmeyer, T. K. Stringham and P. L. Shaver. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology and Management* 61: 359–367.

Carpenter, S. R. 2013. Spatial signatures of resilience. *Nature* 496, 308–309.

Charman, D. J., D. W. Beilman, M. Blaauw, R. K. Booth, S. Brewer, F. M. Chambers, J. A. Christen, A. Gallego-Sala, S. P. Harrison, P. D. M. Hughes, S. T. Jackson, A. Korhola, D. Mauquoy, F. J. G. Mitchell, I. C. Prentice, M. van der Linden, F. De Vleeschouwer, Z. C. Yu, J. Alm, I. E. Bauer, Y. M. C. Corish, M. Garneau, V. Hohl, Y. Huang, E. Karofeld, G. Le Roux, J. Loisel, R. Moschen, J. E. Nichols, T. M. Nieminen, G. M. MacDonald, N. R. Phadtare, N. Rausch, Ü. Sillasoo, G. T. Swindles, E. –S. Tuittila, L. Ukonmaanaho, M. Väliranta, S. van Bellen, B. van Geel, D. H. Vitt, and Y. Zhao. 2012. Climate-related changes in peatland carbon accumulation during the last millennium, *Biogeosciences* 9: 14327 –14364.

Congalton, R. G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment* 37: 35–46.

Dakos, V., and A. Hastings. 2013. Editorial: special issue on regime shift and tipping points in ecology. *Theoretical Ecology* 6: 253-254.

Dickins E. L., A. R. Yallop, and H. L. Perotto-Baldivieso. 2013. A multiple scale of host plant selection in Lepidoptera. *Journal of Insect Conservation* 17: 933–939.

Eppinga, M. B., P. C. De Ruiter, M. J. Wassen, and M. Rietkerk. 2009. Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. *The American Naturalist* 173: 803–818.

Hester, A. J., and G. J. Baillie. 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology* 35: 772 –784.

Holden, J. 2005. Peatland hydrology and carbon release: why small scale process matters. *Philosophical Transactions of the Royal Society A* 363: 2891–2913.

Jerram, R. (2005) Condition assessment for sites of special scientific interest: Armboth Fells SSSI - 2005. Natural England. 29 p.

[JNCC] Joint Nature Conservation Committee. 2009. Common standards monitoring guidance for upland habitats. Version October 2009. Available at: http://jncc.defra.gov.uk/pdf/CSM\_Upland\_jul\_09.pdf. Accessed 25 July 2011.

Lake District Special Planning Board. 1986. Notification of Armboth Fell SSSI. Available at: http://www.sssi.naturalengland.org.uk/special/sssi. accessed 15 July 2011.

Lamers L. P. M., R. Bobbkin, and J. G. M. Roelofs. 2000. Natural nitrogen filter fails in polluted raised bogs. *Global Change Biology* 6: 583–586.

Lucas, R., K. Medcalf, A. Brown, P. Bunting, J. Breyer, D. Clewley, S. Keyworth, and P. Blackmore. 2011. Updating the phase 1 habitat map of Wales, UK, using satellite sensor data. *ISPRS Journal of Photogrammetry and Remote Sensing* 66: 81–102.

MacDougall, A. S., K. S. McCann, G. Gellner, and R. Turkington. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494, 86–89.

Meddens, A. J. H., J. A. Hicke, and L. A. Vierling. 2011. Evaluating the potential of multispectral imagery to map multiple stages of tree mortality. *Remote Sensing of Environment* 115: 1632–1642.

Met Office. 2011. Weather data for Keswick, 2005 to 2010. Available at: http://www.metoffice.gov.uk/forms/education\_weather\_data\_order.html. Accessed accessed 31 June 2011.

Muggeo, V. M. R. 2003. Estimating regression models with unknown break-points. *Statistics in Medicine.* 22: 3055–3071.

Muggeo, V. M. R. 2008. Segmented: an R package to fit regression models with broken-line relationships. *R News*. 8: 20-25

[NSRI] National Soil Resource Institute. 2011a. Full soils site report for location 329044E, 515988N, 4km x 4km. National Soils Resources Institute (NSRI), Cranfield University. Available at: https://www.landis.org.uk/sitereporter/. Accessed 27 May 2011.

[NSRI] National Soil Resource Institute. 2011b. NATMAP vector soilscapes dataset. National Soils Resources Institute (NSRI), Cranfield University. Available at: https://www.landis.org.uk. Accessed July 2011.

Ordnance Survey. 2011. Land-Form PROFILE DTM [NTF geospatial data], Scale 1:25,000, Armboth Fell, Ordnance Survey (GB). EDINA Digimap Ordnance Survey service. Available at: http://edina.ac.uk/digimap. Accessed 15 May 2011.

Palmer, S. C . F. and A. J. Hester. 2000. Predicting spatial variation in heather utilisation by sheep and red deer within heather/grass mosaics. *Journal of Applied Ecology* 37: 616–631.

Perotto-Baldivieso, H. L., E. Meléndez-Ackerman, M. A. García, P. Leimgruber, S. M. Cooper, A. Martínez, P. Calle, O. M. Ramos Gónzales, M. Quiñones, C. A. Christen, and G. Pons. 2009. Spatial distribution, connectivity, and the influence of scale: habitat availability for the endangered Mona Island rock iguana. *Biodiversity and Conservation* 18: 905–917.

Perotto-Baldivieso, H. L., X. Ben Wu, M. J. Peterson, F. E. Smeins, N. J. Silvy, and T. W. Schwertner. 2011. Flooding-induced landscape changes along dendritic stream networks and implications for wildlife habitat. *Landscape and Urban Planning* 99:115–122.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. Available at: www.R-project.org (accessed 20 September 2013).

Reed, M. S., A. Bonn, W. Slee, N. Beharry-Borg, J. Birch, I. Brown, T. P. Burt, D. Chapman, P. J. Chapman, G. D. Clay, S. J. Cornell, E. D. G. Fraser, J. H. Glass, J. Holden, J. A. Hodgson, K. Hubacek, B. Irvine, N. Jin, M. J. Kirkby, W. E. Kunin, O. Moore, D. Moseley, C. Prell, M. F. Price, C. H. Quinn, S. Redpath, C. Reid, S. Stagl, L. C. Stringer, M. Termansen, S. Thorp, W. Towers, and F. Worrall. 2009. The future of the uplands. *Land use Policy* 26: S204–S216.

Rodwell, J. S. 1991. British plant communities, mires and heaths (volume 2). Cambridge, United Kingdom: Cambridge University Press. 628 p.

Rumpff, L., D. H. Duncan, P. A. Vesk, D. A. Keith, and B. A. Wintle. 2011. State-and-transition modelling for Adaptive management of native woodlands. *Biological Conservation* 144: 1224–1236.

Sadler, R. J., M. Hazelton, M. M. Boer, and P. F. Grierson. 2010. Deriving state-and-transition models from an image series of grassland pattern dynamics. *Ecological Modelling* 221: 433–444.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.

Steele, C. M., B. T. Bestelmeyer, L. M. Burkett, P. L. Smith, and S. Yanoff. 2012. Spatially explicit representation of state-and-transition models. *Rangeland Ecology and Management* 65: 213–222.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State-and-transition modelling: an ecological process approach. *Journal of Rangeland Management* 56: 106 –113.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* 24: 271–279.

Thompson, D. B. A., A. J. MacDonald, J. H. Marsden, and C. A. Galbraith. 1995. Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* 71: 163–178.

Twidwell, D., S. D. Fulhendorf, C. A. Taylor Jr., and W. E. Rogers. 2013. Refining thresholds in coupled fire-vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology* 50: 603–613.

[UK NEA] United Kingdom National Ecosystem Assessment. 2011. The UK National Ecosystem Assessment: synthesis of the key findings. Cambridge, United Kingdom: UNEP-WCMC. 87 p.

Wallage, Z. E. and J. Holden. 2011. Near-surface macropore flow and saturated hydraulic conductivity in drained and restored blanket peatlands. *Soil Use and Management* 27: 247–254.

Watson, I. and P. Novelly. 2004. Making the biodiversity monitoring system sustainable: design issues for large-scale monitoring systems. *Australian Ecology*: 29: 16–30.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Rangeland Management* 42: 266–274.

Williamson J., B. T. Bestelmeyer, and D. C. Peters. 2012. Spatiotemporal patterns of production can be used to detect state change across an arid landscape. *Ecosystems* 15: 34–47.

Wilson L., J. M. Wilson, and I. Johnstone. 2011. The effect of blanket bog drainage on habitat condition and on sheep grazing, evidence from a Welsh upland bog. *Biological Conservation* 144: 193–201.

Yallop, A. R., J. I. Thacker, G. Thomas, M. Stephens, B. Clutterbuck, T. Brewer, and C. A. D. Sannier. 2006. The extent and intensity of management burning in the English uplands. *Journal of Applied Ecology* 43: 1138–1148.

FIGURE CAPTIONS

**Figure 1.** Location of Armboth Fell site of special scientific interest in the Lake District National Park in the United Kingdom (inset). The study area consists of four pastures (G1, G2, G3, and G4) with different degrees of grazing (G1, lowest grazing; G4 highest grazing) and was classified into three classes [dwarf shrub heath (DSH). Grassland/degraded wet heath (GDWH), and bare rock). Circles within each pasture represent the sampled areas used to quantify the spatial structure of DSH and GDWH. Great Britain boundaries (EDINA Digimap OS service). Lake District National Park boundaries (© Natural England copyright 2013. Contains Ordnance Survey data © Crown Copyright and database right 2013).

**Figure 2.** Conceptual state-and-transition model for Armboth Fell SSSI, Lake District, United Kingdom. The management impacts (horizontal axis) represent increasing grazing, draining and/or burning. The biophysical factors (vertical axis) refer to changes in slope (increasing), soil moisture (decreasing) and soil organic matter (from deep peat to mineral soils). Ovals represent dominant vegetation states that occur over deep waterlogged peat on the plateau and gentle slopes to thin mineral soils on well-drained steeper slopes (State I: M17 [*Tricophorum cespitosum – Eriophorum vaginatum*], M19 [*C. vulgaris – E. vaginatum*], M20 [*E. vaginatum*]; State II: M15 [*Tricophorum cespitosum – Erica tetralix*]; State III: H10 [*C. vulgaris – Erica cinera*], H12 [*C*. vulgaris – Vaccinium myrtillus], H21 [*C. vulgaris – Vaccinium myrtillus – Sphagnum capillofolium*]; State IV: U6 [*Juncus squarrosus – Festuca Ovina*]; State V: U5 [*Nardus stricta – Galium saxatile*]). Solid arrows indicate threshold transitions reversible with management intervention and dashed arrows are transitions that are autogenically reversible with a reduction in grazing pressure. All transitions incorporate the impact of grazing. Additional factors driving the transitions are drying caused by draining and/or burning (A), drying (by draining and/or burning) and erosion caused by trampling (B) and erosion caused by trampling (C).

**Figure 3.** Dwarf shrub heath (DSH) and grassland/degraded wet heath (GDWH) metrics for the four pastures in the study area: percentage landscape (a, b); mean patch area (MPA; c, d); patch density (PD; e, f), edge density (ED; g, h) and largest patch index (LPI; i, j). Error bars represent the standard error, and letters (a, b, c) indicate statistical differences with a signiﬁcance level of 0.05

**Figure 4.** Fragmentation thresholds in **(a)** dwarf shrub heath mosaic (DSH) and **(b)** grassland/degraded wet heath (GDWH). The dashed vertical line represents the breakpoints calculated using piecewise regression and the shaded area, a homogeneous state dominated by **(a)** Calluna vulgaris and **(b)** gramminoids. The marker at the base of the dashed line represents 95% confidence interval.