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The sheep in wolf‘s clothing? Recognizing threats for land degradation in Iceland using state-and-transition models

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ABSTRACT

Land degradation and extensive soil erosion are serious environmental concerns in Iceland. Natural processes associated with a harsh climate and frequent volcanic activity have shaped Icelandic landscapes. However, following human settlement and the introduction of livestock in the 9th century the extent of soil erosion rapidly escalated. Despite increased restoration and afforestation efforts and a considerable reduction in sheep numbers during the late 20th century, many Icelandic rangelands remain in poor condition. A deeper understanding of the ecology of these dynamic landscapes is needed, and state-and-transition models (STMs) can provide a useful conceptual framework. STMs have been developed for ecosystems worldwide to guide research, monitoring and management, but have been used at relatively small spatial scales and have not been extensively applied to high-latitude rangelands. Integrating the best available knowledge, we develop STMs for rangelands in Iceland, where sheep grazing is often regarded as a main driver of degradation. We use STMs at a country-wide scale for three time periods with different historical human influence, from pre-settlement to present days. We also apply our general STM to a case study in the central highlands of Iceland to illustrate the potential application of these models at scales relevant to management. Our STMs identify the set of possible states, transitions and thresholds in these ecosystems and their changes over time, and suggest increasing complexity in recent times. This approach can help identify important knowledge gaps and inform management efforts and monitoring programmes, by identifying realistic and achievable conservation and restoration goals.

Keywords: adaptive monitoring, land management, sheep grazing, rangeland

Short title: State-and-transition models for rangelands in Iceland

INTRODUCTION

Land degradation and environmental management pose constant challenges to natural resource managers, farmers, researchers and policy makers. Understanding how ecosystems respond to disturbances and management interventions is a fundamental step towards the development of effective management strategies. In this context, state-and-transition models (STMs) can provide a useful conceptual framework to guide monitoring, management and research. STMs synthesize and communicate knowledge about the alternative states of an ecosystem, the causes of state transitions and the presence of thresholds, and offer a framework for research into the processes driving the system (Bestelmeyer *et al.*, 2003; Stringham *et al.*, 2003).

STMs emerged in the context of rangeland management (Westoby *et al.*, 1989) to deal with discontinuities and irreversible transitions in vegetation dynamics in grazing systems, and are typically applied at temporal and spatial scales relevant to management (Bestelmeyer *et al.*, 2003). Beyond rangelands, these models have been widely adopted to synthesize information about state transitions in a variety of terrestrial systems (Jefferies *et al.*, 2006; Spooner & Allcock, 2006). It is now widely recognized that in most systems, changes in vegetation composition are often asymmetric and abrupt transitions can occur between alternative vegetation states (Suding *et al.*, 2004). For example, in rangelands the activities of herbivores can interact with physical processes leading to discontinuous and non-reversible transitions. Herbivores can initiate small changes to plant-soil systems that trigger positive feedbacks leading to rapid catastrophic shifts in vegetative states and irreversible changes in soil properties (Jefferies *et al.*, 2006; Van de Koppel *et al.*, 1997).

Most Icelandic ecosystems are used as extensive summer rangelands and sheep grazing is often considered a main driver of land degradation. Extensive soil erosion in some parts of the country has been associated with human settlement and the introduction of livestock grazing, coupled with harsh environmental conditions and frequent volcanic activity (Arnalds, 1987). Intensive grazing and trampling by large mammals can disrupt vegetation cover and expose bare ground to erosion by wind and water. In Iceland, the volcanic origin of soils (Andosols) makes them highly susceptible to erosion, especially on younger soils within the volcanic active zone and at higher elevation in the highlands (Arnalds, 2015). Once bare ground is exposed, positive feedbacks are initiated that can lead to accelerated erosion processes (Aradóttir *et al.*, 1992). The concept of thresholds has been applied in Iceland to describe this catastrophic shift where ecosystems collapse into a degraded state (Aradóttir *et al.*, 1992; Archer & Stokes, 2000), and the only attempt to apply STMs to Icelandic ecosystems also focused on this transition (Thorsson, 2008).

However, “less catastrophic” transitions are also likely; they may imply less obvious changes in the structure and function of the ecosystem, but may still have important management implications if the ability of the alternative states to provide valuable ecosystem services declines. Evidence for the occurrence of these thresholds is found in systems that fail to recover after removal of disturbance, for example when excluding grazing does not trigger changes leading to recovery. Once the system has shifted into an alternative state, releasing grazing pressure alone may not be sufficient to revert back to the previous state and intensive management actions, such as seeding or shrub control, may be required (Bestelmeyer *et al.*, 2003). Such examples are relatively common in Iceland (Marteinsdóttir *et al.*, 2017). For example, in some rangelands in the highlands no apparent plant community responses were detected after four years of grazing protection (Jónsdóttir *et al.*, 2005). Even when longer time periods were considered in areas where grazing had been abandoned for >60 years, plant diversity did not differ from continuously grazed areas (Mörsdorf, 2015).

Our objective is to produce a state-and-transition modelling framework for rangelands in Iceland, to help understand landscape changes brought about by human settlement and human activities, relative to other drivers of change (climate fluctuations and environmental disturbances, such as volcanism), and to guide research, monitoring and management. We apply such framework at a large spatial and temporal scale, focusing on three periods with different human influence: before human settlement in the late 9th century (pre-landnám), until 1900s (pre-industrial period) and after 1900s. Iceland provides a unique opportunity to try to disentangle the influence of different drivers of landscape change, because human influence can be clearly tracked in the paleoenvironmental record and historical narratives. Here, we expand on the models for birch woodland degradation in Iceland (Aradóttir *et al.*, 1992; Archer & Stokes, 2000; Thorsson, 2008) to incorporate all possible vegetation states present and past, and describe the potential transitions and thresholds between them. To illustrate the usefulness of such a framework we apply the post-1900s STM to a case study in the highlands of Iceland at a finer spatial scale that is more relevant to management.

METHODS

STMs are conceptual frameworks constructed around distinct ecosystem states and their possible changes (transitions) under a given set of environmental drivers (e.g. disturbances). Narrative descriptions in STMs are generally supported by different sources of data, from informal historical observations and expert knowledge to controlled experiments (Bestelmeyer *et al.*, 2009). To build the general STM framework for Iceland we used a recent compilation on the ecological impacts of sheep grazing in Iceland (Marteinsdóttir *et al.*, 2017), paleoecological evidence, historical records and expert knowledge (for more details and specific sources see **Tables S1 and S2**).

The basic unit of STMs are the different ecosystem states (S), which are broadly characterized by their vegetation structure and composition, the dominant ecosystem processes and their main ecosystem attributes (Stringham *et al.*, 2003); as such, states reflect land potential and are broadly defined by topography, climate and soil characteristics. Generally, states are defined as units that are stable within periods of time and spatial scales (e.g. 0.1-10 ha) relevant to land management (Bestelmeyer *et al.*, 2003); in our study however, we define states more broadly to encompass larger spatial and temporal scales (e.g. Walker & Westoby, 2011; Zhang *et al.*, 2018). To build our general STM, we recognized different states for rangelands in Iceland based on broad, structurally distinct habitat types (Ottósson *et al.*, 2016; **Figure 1**). States include different plant communities and dynamic soil properties (community phases).

Contrary to the shifts among community phases (pathways) within a state, transitions (T) between states are usually not reversible by simply altering the intensity or direction of the factors that produced the change. Transitions may be gradual and cumulative, or non-linear and characterized by abrupt thresholds. Here, the thresholds define the point beyond which ecological processes cannot maintain the sustained equilibrium of the state any longer (Stringham *et al.*, 2003). Based on the best available knowledge we identified all possible transitions between the different ecosystem states and hypothesized the factors driving them, for different time periods.

We separated our analyses into three different historical periods with contrasting human influence: 1) before human settlement, 2) until 1900s (pre-industrial period) and 3) after 1900s. Shortly before settlement, a volcanic ash layer was deposited almost everywhere in Iceland (Þórarinsson, 1961). This Landnám tephra layer provides a precise litho-chrono-stratigraphic marker of human colonization in the paleoenvironmental record, and facilitates the definition of the 'paleoanthropocene' in Iceland, as a period of pre-industrial human influence (Streeter *et al.*, 2015). Analyses of pre-settlement vegetation in Iceland are based on pollen assemblages preserved in lake sediments and peat (Hallsdóttir, 1995), macrofossil record and sediment analyses (Eddudóttir *et al.*, 2016; Vickers *et al.*, 2011). In addition to the paleoenvironmental record, information on vegetation patterns after landnám is also available from historical documents, like the Old Icelandic Sagas.

Case study: Auðkúluheiði

We applied the post 1900s STM model to the rangelands in Auðkúluheiði to illustrate the ability of our model to accommodate local case studies at spatial and temporal scales relevant to management. Auðkúluheiði is a commons grazing area located in the northwest-central highlands of Iceland (65°16'N, 20°15'W) at 480 m elevation, about 150 m above the potential tree line. The area is outside the volcanic active zone on basaltic bedrock with loose glacial deposits. Soils are well-drained Andosols with high cation exchange capacity and high water retention (Arnalds, 2015). Climate is oceanic-subarctic-alpine, with an average annual temperature of 0.3°C and 397 mm of annual precipitation. Paleoecological information for the area is available from Barðalækjartjörn, a lake on the north boundary of the communal grazing land (Eddudóttir *et al.*, 2016). The grazing lands in Auðkúluheiði are highly valued and a considerable amount of research has been conducted in the area (Jónsdóttir, 1984; Magnússon & Magnússon, 1992).

RESULTS

The general STMs increased in complexity with time, from the simplest pre-landnám model to the most complicated present situation (**Figures 2-4**). We defined 8 possible ecosystem states and 11 potential transitions (**Table 1**). Transitions were grouped when they represented the same process; for example, primary succession on barren lands (**T7**) could lead to moss/lichen dominated fields (**T7a**), birch woodlands (**T7b**), wetlands (**T7c**), heathlands (**T7d**) or grasslands (**T7e**), depending on environmental conditions, topography and substrate properties (**Table 1**).

Pre-landnám period

Pollen of mountain birch (*Betula pubescens* Ehrh.) has been used as a proxy for the extent of birch woodlands (**S1**; **Figure 2, Table 1**) in the paleoenvironmental record of Iceland. During the Holocene birch woodlands were common in Iceland, but their extent fluctuated with variations in climate (Erlendsson & Edwards, 2009; Hallsdóttir, 1995). The cover of birch woodland at the time of settlement has been estimated to be somewhere between 8% (Ólafsdóttir *et al.*, 2001) to 40% of the country (Bjarnason, 1971), with the most recent estimate of 24% (Wöll, 2008). Before human influence, colder periods drove transitions from woodland to open landscapes (**T1, T3, T5**) dominated by wetland (**S2**) or heathland vegetation (**S3**), depending on topography. Grasslands (**S4**) may have also occured on moister soils above the treeline. Natural catastrophic events, like volcanic activity or glacial floods may have created barren lands (**S5**) that would have acted as new primary successional habitats. Thus, without the influence of humans and large herbivores, pre-settlement vegetation patterns were likely determined by topography and substrate properties, and responded mainly to fluctuations in climate and aeolian processes (Eddudóttir *et al.*, 2016) and, on shorter time scales, to volcanism.

Although there is no clear evidence in the paleoenvironmental record, a likely primary successional stage are fields dominated by mosses or lichens (**S6**). This state dominates many primary successional habitats today, such as lava flows and glacier forelands (Cutler *et al.*, 2008; Vilmundardóttir *et al.*, 2015).

From landnám to 1900s

Paleo- and archeological records provide evidence for dramatic human impact on the environment shortly after settlement (Dugmore *et al.*, 2005; Eddudóttir *et al.*, 2016; Streeter *et al.*, 2015). For example, in the lowlands, extensive clearing of birch woodlands in combination with livestock grazing, resulted in a rapid transition to open grasslands (**T5**) and dwarf shrub heathlands (**T4**) that were less resilient to natural catastrophes (Dugmore *et al.*, 2005; Vickers *et al.*, 2011). These changes are most evident around farms (Erlendsson & Edwards, 2010; Kristinsson, 1995) and in more densely populated areas (Þórarinsson, 1961).

The onset of human activity in Iceland was combined with a colder period, the Little Ice Age (1450 to 1920), which implied more rapid declines in vegetation cover than before settlement (Haraldsson & Ólafsdóttir, 2003). This colder period also implied that people‘s livelihoods became more dependent on livestock than during the settlement period (Haraldsson & Ólafsdóttir, 2006). The number of animals that could be sustained depended partly on the availability of food during winter, either through access to winter grazing areas or haymaking during summer (Arnalds & Barkarson, 2003). Historical winter grazing contributed significantly to accelerated land degradation close to some farms (Simpson *et al.*, 2004), as livestock offtake of vegetation would almost always exceed vegetation productivity in winter. Towards the end of this period, ploughing and harrowing allowed the expansion of grassland and cultivated hay meadows (**S4**) (Þórhallsdóttir *et al.*, 2013).

The number of sheep began to increase in the 1820s when foreign markets opened up for sheep products (Þórhallsdóttir *et al.*, 2013). Simultaneously, traditional grazing practices changed; the shift in interest from milk and dairy products to meat in the second half of the 19th century meant that ewes no longer needed to be grazed close to the farm so that they could be milked daily, and extensive summer grazing in the highlands became more common (Þórhallsdóttir *et al.*, 2013). Consequently, the grazing pressure in highland ranges increased considerably towards the end of the 19th century. Overgrazing in some areas may have led to the formation of landscapes dominated by soil erosion spots (Archer & Stokes, 2000). These degraded areas (**S7**) represent a transitory state (*sensu* Westoby *et al.*, 1989) that is highly unstable and leads to accelerated erosion and eventually the formation of barren areas.

Post-1900s

Human population in Iceland has steadily increased since the late 1890s (Haraldsson & Ólafsdóttir, 2006). Improved technology in haymaking and the introduction of artificial fertilizers allowed the numbers of sheep to increase, reaching a maximum of 896,000 animals in 1977 (Arnalds & Barkarson, 2003). A livestock quota was introduced in 1985 but by the time the stocking rates were reduced, the ecosystems in many grazing commons had already shifted to a severely degraded state (**S5**). The numbers of sheep are nowadays half of those in the early 1980s but are still high relative to historical abundances (Marteinsdóttir *et al.*, 2017). In parallel, improved access to winter fodder led to the gradual abandonment of winter grazing, reducing grazing pressure around farms. Still, the recovery of vegetation in many areas after the release in grazing pressure is slow (Bjarnason, 1971; Magnússon & Svavarsdóttir, 2007).

From the perspective of land management and environmental protection the onset of the 20th Century implied great changes. Nation-wide efforts to halt soil erosion and subsequent sand encroachment began in the early 1900s. A new law on soil conservation, revegetation and afforestation was passed in 1907, leading to the foundation of two state institutions, the Soil Conservation Service and the Forestry Service (Magnússon, 2000). Considerable revegetation of barren areas (**T7**) has been achieved, but afforestation, and some revegetation efforts, also created a new man-made state, plantations (**S8**), dominated by introduced species.

Organised measures to halt soil erosion and reclaim eroded land through controlled revegetation of eroded areas started in the early 1900s (Magnússon, 2000; Olgeirsson, 2007). Commonly used methods involved fertilizing and sowing of agronomic grasses (e.g. *Festuca rubra, Phleum pratense, Deschampsia beringensis* and *Lolium multiflorum*) or native species, such as Lyme grass (*Elymus arenarius*) or to a lesser extent, *B. pubescens* or *Salix* sp. shrubs. Other reclamation activities involved fencing off areas to exclude grazing (Magnússon & Svavarsdóttir, 2007), and from the early 1990s using fertilizers alone, or planting introduced species like the Nootka lupine (*Lupinus nootkatensis*). The lupine was introduced to Iceland in the 1940s for revegetation purposes (Magnusson, 2010), however it was not used on a large scale until after the Soil Conservation Service of Iceland started to produce seed in the 1980s (Arnalds, 1988). Since then, the lupine has spread greatly especially in disturbed habitats in the lowlands, but also encroaching into dwarf-shrub heathlands (**T11b** in **Figure 4**), to the extent that it is now classified as an invasive species in Iceland (Magnusson, 2010).

In the early days the main purpose of revegetation was to control soil erosion, rather than to direct plant succession to specific pathways (Aradóttir *et al.*, 2013). In the 1950s, due to the availability of new technology, the emphasis shifted to the cultivation of grass on eroded land (**T7e** in **Figure 4**), using commercial grass seeds and artificial fertilizers (Greipsson & El-Mayas, 1999), with the aim of hay production and rangeland improvement (Magnússon, 2000). After the mid 1980s an ecological approach to revegetation was adopted, and greater emphasis was put on the development of sustainable ecosystems (Aradóttir *et al.*, 2013; Magnússon, 2000).

During the early 1900s forestry efforts focussed on preserving the remaining birch woodlands (Aradóttir & Eysteinsson, 2005), the cover of which during that period has been estimated to be 1% of the country (Traustason & Snorrason, 2008). Efforts to protect native birch woodland remnants date back to an act that was passed in 1899 to protect the woodlands; the first national forest, Hallormsstaðaskógur was fenced off in 1905-1908 (Bjarnason, 1971). Planting of exotic conifers started in the late 1930s. The government has supported afforestation on farms since 1970, which has led to the transition of many grasslands (**T11c**) and to a lesser extent heathlands, to forest plantations (**T11b**). Most forest plantations were carried out on deforested areas, but in some places tree planting took place within natural birch woodlands (**T11a**) (Traustason & Snorrason, 2008).

Recent greening trends in some parts of Iceland (increases in NDVI) during 1982-2002 (Raynolds *et al.*, 2015), the expansion of non-native species, like planted conifers or the invasive Nootka lupine (Icelandic Institute of Natural History, unpublished data), and increases in cover of birch woodland from 1.1 in 1989 to 1.5% in 2012 (Snorrason *et al.*, 2016) are likely related to reductions in grazing, extensive revegetation and afforestation efforts as well as climate warming and natural vegetation succession in areas of glacial retreat (Raynolds *et al.*, 2015; Vilmundardóttir *et al.*, 2015).

Case study: Auðkúluheiði

Early Holocene records (10,300 to 8,000 cal. a BP) for Auðkúluheiði suggest the dominance of dwarf shrub heathlands (**S3**) in the area, dominated by *Betula nana*, *Salix* sp. and *Juniperus communis*, together with wetlands (**S2**) and sparsely vegetated rocky/sandy surfaces (**S5**) (Eddudóttir *et al.*, 2016). Birch woodlands may have expanded from lower elevations during a warmer period in the Holocene, but at the time of settlement landscapes were already dominated by dwarf shrub heathlands (Eddudóttir *et al.*, 2016). The introduction of grazing livestock reduced the resilience of the ecosystem to volcanism and a cooling climate during the Little Ice Age, as evidenced by increased soil erosion rates from the 9th Century (Eddudóttir *et al.*, 2016).

The Auðkúluheiði commons have been extensively used as a summer rangeland for centuries (Jónsdóttir, 1984; Magnússon & Magnússon, 1992). Indications of the natural vegetation of the heathlands without the influence of grazing in this area are available from lake islands to which sheep have never had access (Jónsdóttir, 1984; Kristinsson, 1979). Some species like *Angelica archangelica* were only found on the islands, while others, like *Geranium sylvaticum* or tall native willow shrubs (*Salix* spp.) were less abundant in the grazed areas (Kristinsson, 1979). Differences between grazed and non-grazed heathland vegetation were more pronounced where growing conditions for plants were more favourable (Jónsdóttir, 1984). Nowadays the landscape is dominated by extensively grazed heathlands (**S3**, **Figure 5**) and degraded (**S7**) and barren areas (**S5**). Wetlands (**S2**) occur in depressions, and grasslands (**S4**) are restricted to managed areas close to old shieling areas or restoration sites (Thorsteinsson, 1991). Moss (**S6**) dominates ridgetops that are not fully eroded (Jónsdóttir, 1984).

The post-1900s general STM (**Figure 4**) can be simplified to accommodate local case studies such as Auðkúluheiði (**Figure 5a**). Because the model is applied to a smaller spatial and temporal scale, it can be used to more directly infer how management would affect changes in the ecosystem over time (**Figure 5b**). In the absence of grazing, the amount of exposed bare ground may vary with topography and exposure, but is generally small (<10% on average; Jónsdóttir, 1984). If sheep are present, the percentage of bare ground is likely to increase over time, as trampling and selective foraging can disrupt vegetation cover, creating bare ground patches that are open to erosion. It has been suggested that when exposed areas exceed 35% of the surface (Thorsson, 2008), feedbacks will be initiated that lead to irreversible transitions of the landscapes to degraded states (**S7**) and ultimately to barren lands (**S5**). This threshold value, however, needs to be taken with caution, as it is based on a single estimate (Thorsson, 2008) and is likely to vary with topography and exposure.

How quickly this stage is reached will depend on sheep densities; at high sheep densities the threshold will be crossed earlier than at moderate sheep densities; under light grazing pressure this threshold may not be crossed at all. Management interventions are likely to take place only when certain amount of exposed bare ground is detected in the landscape (“bg1“ in **Figure 5b**), which will occur earlier under high grazing pressure (t_1) than under moderate grazing pressure (t_3). At this point, reducing sheep densities from high to moderate grazing pressure (trajectory a) will delay crossing the functional threshold; strongly reducing grazing pressure from high or moderate to low sheep densities (trajectories b and b_1) will maintain the amount of exposed soil, while completely excluding sheep (trajectories c and c_1) could slowly reduce the amount of bare ground. The original state without grazing (heathland) may not be completely reversed within management time frames (e.g. Jónsdóttir *et al.*, 2005), possibly because of the lack of propagules of palatable species that have been kept at very low abundance as a result of centuries of grazing. Finally, once the functional threshold is passed, reducing or excluding sheep grazing alone will not restore the vegetated state (trajectory d), and more costly interventions, such as seeding and fertilization, would be needed to restore vegetation cover (Thorsteinsson, 1991).

DISCUSSION

We developed state and transition models for rangelands in Iceland, at a large spatial scale, for historical periods with increasing human influence. Typically, STMs are applied at smaller spatial scales that are relevant to land managers, but we find the use of STMs at broader spatial and temporal scales provides a novel approach for better understanding of the forces driving the system and how they interact. The history of human colonization in Iceland and a reasonably good documentation through the paleaoenvironmental record and historical documents allowed constructing models for periods with different human influence at a country-wide scale. Our models indicate increasing complexity over time, with human influence creating new states and accelerating some transitions. Human impacts can widen the range of habitats in which threshold dynamics can occur (Suding & Hobbs, 2009). In Iceland, up to the 1900s, human influence accelerated landscape degradation. Although mitigation efforts increased at the turn of the century, extensive soil erosion had already become (and continues to be) the main environmental problem in Iceland (Arnalds, 2005).

Long-term, sustained stresses, such as gradual changes in climate or grazing, can act as directional forcings for incremental state transitions. Herbivores can drive transitions between ecosystem states in tundra ecosystems (Van der Wal, 2006). For example, Zimov et al (1995) postulated that at the end of the Pleistocene in Beringian ecosystems the large-scale transition from productive grass-dominated steppe to unproductive moss-dominated tundra could be attributed to the extinction of Pleistocene mega-herbivores. The influence of human management through extensive sheep grazing is evident in landscapes throughout the North Atlantic region (Ross *et al.*, 2016). The term "ovigenic landscape" (Buckland & Dugmore, 1991) has been used to describe the historical impact of sheep grazing on Icelandic ecosystems, where extensive sheep grazing has been linked to land degradation (Arnalds, 1987). The impacts of grazing in Iceland might be particularly severe, as volcanic soils are particularly prone to water and wind erosion; once bare ground is exposed active soil erosion can become the dominant process in the landscape (Arnalds, 2015). In addition to these long-term forcings, episodic perturbations can drive rapid transitions with unpredictable outcomes (Archer & Stokes, 2000). This might be the situation in Iceland, where grazing pressure is compounded by climate and stochastic environmental disturbances, such as volcanic eruptions. Some species are more sensitive to volcanic ash and aeolian deposition (Vilmundardóttir *et al.*, 2009), processes that can suffocate vegetation and accelerate subsequent erosion.

Generating a single model for an entire country and for a long time frame entails a considerable degree of simplification. However, the simplicity of STMs is also one of their main strengths, as it facilitates the use of these models as a communication tool (Grice & MacLeod, 1994) and helps organizing our knowledge about a system (Bestelmeyer *et al.*, 2003). To guide decision-making and management more detailed models at finer spatial and temporal scales are needed, as well as an acknowledgement of where and when some transitions are likely to happen (i.e. land potential). The application of our STM to a grazing common in the central highlands of Iceland illustrates how the general model can be adapted to particular situations and the usefulness of this approach to guide management efforts. For example, our model suggests that management actions at different times will require different intensity of management interventions to achieve the desired restoration outcomes. Once thresholds have been passed, restoration may become prohibitively expensive and with lesser probability of success. More intensive interventions may be needed to lead to state changes, and research efforts could be directed to specific restoration actions. For example, in Iceland the expansion of birch forests is limited by the isolation of patches and availability of seed sources, so it has been suggested that actively establishing discrete patches of woodland scattered across the landscape could facilitate natural recolonization by birch (Aradottir & Halldorsson, 2017).

Our application of the general STM to a specific case study also illustrates the usefulness of these approaches for environmental monitoring and the assessment of current land condition. By linking specific indicators to STMs model developers can provide tools to help managers determine the state that land is in, relative to its potential, and evaluate the probablity of a transition (Bestelmeyer *et al.*, 2003, 2009). For example, the amount of bare ground seems to be an important indicator for catastrophic transitions in Iceland (Aradóttir *et al.*, 1992; Thorsson, 2008). Other variables, like moss depth, through its influence on vascular plants and soil properties (Gornall *et al.*, 2007), might be indicative of state changes that do not necessarily imply irreversible ecological thresholds. Different community attributes may respond differently to grazing and climatic variability, so evaluation of a broad set of vegetation variables would provide a more thorough interpretation of vegetation dynamics (Fernandez-Gimenez & Allen-Diaz, 1999; Fuhlendorf *et al.*, 2001). However, as resources are often limited only a subset of variables can be monitored; selection of these variables should be guided by specific research questions and the best available knowledge of the system (Lindenmayer & Likens, 2009).

In sum, STMs provide a solid framework that can be applied at broader spatial and temporal scales to organize knowledge about a system and its main drivers of change. By including time periods before and after human settlement in Iceland, our models allow identifying landscape changes brought about by human activities including (but not restricted to) sheep grazing, relative to other drivers of change, such as climate fluctuations and environmental disturbances. Increased complexity over time suggests that human activities have a profound influence on landscape changes. These models also help put into perspective the perceived damaging effect of sheep grazing on Icelandic ecosystems and how management can alleviate or worsen these effects (i.e. the sheep in wolf's clothing). Identifying the potential drivers of ecosystem transitions and where they are likely to be more influential is a critical step to inform management practices, especially when drivers are related to land uses (e.g. grazing practices), because these drivers can be more easily managed than others (e.g. climate-related changes).

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TABLES

Table 1. Description of ecosystem states (S) in Iceland and possible transitions (T) between states and their potential drivers, as shown in Figures 2-4. Note that drivers are different and act over different time-scales for each of the models. For more details on each state and transition and relevant references see Tables S1 and S2. Correspondence with the habitat types described by Ottóson et al (2016) are indicated for each state.

State	Description		Habitat type
S1	**Birch woodland**	Mountain birch (*Betula pubescens*) forests generally have a lush herbaceous ground cover. Potential treeline is determined by altitude (summer temperature) and proximity to the coast (i.e. less continental climate).	L11 Woodlands
S2	**Wetland communities**	Wetlands are dominated by sedges, rushes and graminoids. Wetlands occur in depressions where ground water reaches the surface, or on areas with less permeable bedrock. Depending on hydrology and the presence of species adapted to drier conditions, saturated and damp wetlands can be distinguished.	L8 Wetlands
S3	**Heathlands**	Heathlands are dominated by shrubs, perennial graminoids and occasionally mosses. Heathlands are determined climatically (i.e. above treeline) or by human practices (e.g. clear-cutting). Grazing can change the composition of heathlands, from heathlands dominated by palatable species like *Salix* sp. shrubs, to heathlands dominated by less palatable species like dwarf birch (*Betula nana*).	L10 Heathlands
S4	**Grassland communities**	Grasslands are dominated by grasses and other graminoids. They are to a large extent related to human uses (sheep grazing) in Iceland, but they may occur naturally above treeline on moister soils than heathlands.	L9 Grasslands
S5	**Barren areas**	Areas with very sparse vegetation cover (<5%) where only the mineral surfaces, glacial till or frost-heaved gravel remain. This state includes also deserts and other primary succession habitats.	L1 Fell fields, morraines and sands; L2 Exposed aeolian soils
S6	**Moss/lichen dominated fields**	The occurrence of thick moss carpets may be topographically determined (e.g. on some ridgetops), or on primary successional habitats such as lava flows.	L5 Moss lands; L6 Lava fields
S7	**Degraded areas**	This state is the result of increased abundance and size of soil erosion spots in woodlands (**S1**), heathlands (**S3**) or grasslands (**S4**), generaly as a result of inadequate management. This is a transient state (*sensu* Westoby *et al.*, 1989) that will change rapidly into barren areas once active erosion processes are in place.	L2 Exposed aeolian soils
S8	**Plantations**	Man-made patches involving non-native species that become persistent in the landscape, either for reclamation or forestry.	L14 Other land types

Transitions		Potential drivers
T1	**S1 → S2**	Changes in hydrological regimes caused for example by retreat of glaciers due to climate changes, and human intervention (e.g. in some areas clearcutting can cause the water table to rise because ground water levels are no longer suppressed by woody vegetation after trees are removed). This transition is unlikely on decadal time-scales.
	S2 → S1	The transition from wetlands to woodlands would require changes in hydrological regimes. This transition is unlikely on decadal time-scales.
T2	**S2 → S3**	Prolonged droughts or human intervention (drainage).
	S3 → S2	Prolonged periods of high rainfall and alteration of surface or subsurface water flow and soil moisture. These changes could be driven by hydrological changes associated to glacial recession can raise the water table and form bogs, or by human efforts to restore wetlands, but in general this transition is unlikely on decadal time-scales..

T3	**S2 → S4**	Natural changes in hydrological regimes, or human intervention (drainage).
	S4 → S2	Same as T2 (transition from heathlands to wetlands).
T4	**S1 → S3**	Changes in climate that cause treeline recession, and human intervention either through deforestation and/or grazing on well-drained soils.
	S3 → S1	Changes in climate towards warmer conditions can lead to the expansion of birch woodlands. Restoration of birch woodlands on heathland can be achieved through fencing off sheep and horses; regeneration of birch woodlands can be accelerated by planting and sowing.
T5	**S1 → S4**	Changes in climate that cause treeline recession, for example during colder periods, and human intervention either through deforestation and/or grazing on moister soils.
	S4 → S1	Changes in climate towards warmer conditions can lead to the expansion of birch woodlands given that seed sources are available. Protection from grazing can also favour this transition.
T6	**S3 → S4**	Changes in soil conditions (increase in soil moisture due to for example altered precipitation regimes), grazing or active human management (shrub clearing, fertilization) could reduce the amount of shrubs. In heathlands where mosses are dominant, livestock trampling could favour changes towards graminoid-dominated states.
	S4 → S3	Grazing abandonment and changes in climate (warming) could lead to shrub expansion.
T7	**S1, S2, S3, S4, S6 → S5**	Catastrophic events (e.g. volcanic eruptions, glacial river floods) and enhanced aeolian processes (e.g. sand encroachment) that cause vegetation die-off, opening of bare ground patches and subsequent soil erosion. Adverse climatic conditions, like colder periods, can intensify the effect of grazing and other disturbances (e.g. frequent tephra deposition, sand encroachment, glacial river floods) promoting the formation of barren areas.
	S5 → S1, S2, S3, S4, S6	Primary succession occurs under favourable climatic conditions for the establishment of vegetation (e.g. increased snow cover in winter that reduces the frequency of freeze-thaw cycles, and warm summers with sufficient precipitation). In many cases, primary succession will occur over time-scales longer than decades. Protection from grazing and climate warming, as well as restoration and revegetation efforts can accelerate this transition.
T8	**S6 → S1, S3, S4**	Opening gaps in the moss layer, or reducing its thickness through trampling can allow the establishment of other species, such as graminoids, leading to changes in plant community composition.
T9	**S1, S3, S4, S6 → S7**	Trampling and plant consumption by livestock disrupts the plant biomass thermal barrier that amplifies freeze-thaw dynamics destabilizing the highly erodible andosol soils and making them more prone to frequent, small scale disturbances associated with frost boils, frost heaving and needle-ice formation.
	S7 → S1, S3, S4, S6	Considerably reduced or no grazing and climatic conditions favourable for the establishment of vegetation (e.g. increased snow cover in winter that reduces the frequency of freeze-thaw cycles, and warm summers with sufficient precipitation). This transition involves a functional threshold, so it is not easily reversed, especially over decadal time-scales.
T10	**S7 → S5**	This transition is unidirectional in a decadal time-scale. A positive feedback is initiated where rates of expansion of eroded patches increase with increasing patch size. Surfaces and escarpments create active *erosion fronts* whose vertical faces (rofabards) are fully exposed to further wind and water erosion.
T11	**S1, S2, S4, S5 → S8**	Afforestation or reclamation efforts and natural expansion of plantations.
	S8 → S1, S2, S4, S5	Natural dieback because of climatic mismatch of planted trees, disease (e.g. larch dieback or the pine wooly aphid), or natural recession of some patches of Nootka lupine and human efforts to eradicate invasive species.

FIGURE CAPTIONS

Figure 1. Representative photos of the eight different terrestrial ecosystem states identified in this study for rangelands in Iceland.

Figure 2. State-and-transition models for the time before settlement (pre-landnám) in Iceland. Possible ecosystem states (S) are indicated by boxes and transitions (T) are shown as the arrows connecting the boxes; arrow thickness suggests the probablility of each transition. Drivers of transitions in this model act over long time-scales. Within each state, several community phases (shaded boxes) and community pathways (dotted arrows) might be possible. The functional threshold (dashed line) indicates an irreversible transition. See Tables 1, S1 and S2 for detailed descriptions of states and transitions.

Figure 3. State-and-transition models for the time between landnám and 1900s. Human settlement in Iceland (landnám) brought livestock grazing, clearcutting and agricultural use mostly of lowland areas for haymaking and cereal production. See Figure 2 for details; transitions mediated by grazing are indicated with sheep symbols. Thickness of the arrows suggests the likelihood of the transitions; note changes from previous period. Drivers of transitions in this model act over intermediate time-scales (i.e. centuries).

Figure 4. State-and-transition models for the time post-1900s. Soil erosion and land degradation became a main environmental concern in Iceland in the early 1900s, when restoration and reforestation efforts began (e.g. establishment of the Soil Conservation Service of Iceland in 1907). Drivers of transitions in this model act over decadal time-scales (see Table 1 and S2). Arrows acknowledge the possibility of a transition between two states; some transitions may occur with a very low probability (e.g. only under certain conditions of topography, climate or soil type), or are highly unlikely at this time-scale (indicated by thin arrows). See Figure 2 for details; transitions mediated by grazing are indicated with sheep symbols.

Figure 5. Simplified state-and-transition model for summer rangelands in Auðkúluheiði, in the central highlands of Iceland based on the post-1900s model (a), and proposed changes over time in the relative cover of bare ground cover (as a proxy for land degradation) in response to different management interventions (b). Over time, sheep grazing increases the area of exposed bare ground (solid lines; intensity of grazing pressure is indicated by the number of sheep symbols). When exposed areas exceed 35% (dashed orange line; functional threshold and upper limit for S3, the heathland state) feedback processes will lead to irreversible transitions towards degraded states (S7) and, ultimately, barren lands (S5). Different ecosystem trajectories (discontinuous blue lines) will follow management interventions (red dots), such as reducing to moderate (trajectories a) or low (trajectory b) grazing pressure, or totally excluding grazing (trajectory c), implemented at different points in time (t_1, t_2, t_3). Once the functional threshold is crossed, reducing or excluding sheep grazing alone will not restore the vegetated state, and more costly interventions, such as seeding and fertilizing, would be needed to restore vegetation cover (trajectory d).