

Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient

INGER ELISABETH MÅREN,^{1,4} JUTTA KAPFER,² PER ARILD AARRESTAD,³ JOHN-ARVID GRYTNES,¹ AND VIGDIS VANDVIK¹

¹Department of Biology, University of Bergen, Thormøhlensgate 53A, 5007 Bergen Norway

²Norwegian Institute of Bioeconomy Research, Holtveien 66, 9016 Tromsø Norway

³Norwegian Institute for Nature Research, Thormøhlensgate 55, 5008 Bergen Norway

Abstract. Successional dynamics in plant community assembly may result from both deterministic and stochastic ecological processes. The relative importance of different ecological processes is expected to vary over the successional sequence, between different plant functional groups, and with the disturbance levels and land-use management regimes of the successional systems. We evaluate the relative importance of stochastic and deterministic processes in bryophyte and vascular plant community assembly after fire in grazed and ungrazed anthropogenic coastal heathlands in Northern Europe. A replicated series of post-fire successions ($n = 12$) were initiated under grazed and ungrazed conditions, and vegetation data were recorded in permanent plots over 13 years. We used redundancy analysis (RDA) to test for deterministic successional patterns in species composition repeated across the replicate successional series and analyses of co-occurrence to evaluate to what extent species respond synchronously along the successional gradient. Change in species co-occurrences over succession indicates stochastic successional dynamics at the species level (i.e., species equivalence), whereas constancy in co-occurrence indicates deterministic dynamics (successional niche differentiation). The RDA shows high and deterministic vascular plant community compositional change, especially early in succession. Co-occurrence analyses indicate stochastic species-level dynamics the first two years, which then give way to more deterministic replacements. Grazed and ungrazed successions are similar, but the early stage stochasticity is higher in ungrazed areas. Bryophyte communities in ungrazed successions resemble vascular plant communities. In contrast, bryophytes in grazed successions showed consistently high stochasticity and low determinism in both community composition and species co-occurrence. In conclusion, stochastic and individualistic species responses early in succession give way to more niche-driven dynamics in later successional stages. Grazing reduces predictability in both successional trends and species-level dynamics, especially in plant functional groups that are not well adapted to disturbance.

Key words: bryophytes; burning; *Calluna vulgaris*; coexistence; conservation management; determinism; disturbance; grazing; heathland; randomization test; stochasticity; vascular plants.

INTRODUCTION

Ecological succession is an important process in natural as well as anthropogenic landscapes (Drake 1990, Glenn-Levin et al. 1992, Pickett and Cadenasso 2005, Hobbs et al. 2007, Pickett et al. 2008). Local community species assembly during succession may be driven by deterministic or stochastic processes (e.g., Kreyling et al. 2011, Helsen et al. 2013, Hidding et al. 2013, Raavel et al. 2013, Bhaskar et al. 2014), or by a combination of both (e.g., Gravel et al. 2006, Adler et al. 2007). The relative importance and temporal dynamics of these different processes over succession and in different systems, as well as what drives this variation, is not well understood (Chase 2010, Chase and Myers 2011, Zhou et al. 2014).

This conundrum has its roots in the early work on ecological succession where Clements (1916) describes succession as a largely deterministic process of predictable species, niche, and vegetation replacements, whereas Gleason (1926) and Eliot (2007) focus more on succession as an outcome of stochastic processes and individualistic responses of species to their environment. The neutral paradigm (e.g., Hubbell 2001, Chu et al. 2007, Zhou et al. 2014) adds another dimension to the stochastic perspective by illustrating how many of the patterns that we observe in nature, including succession, may emerge not only under high stochasticity but also in the absence of any differences among species in their responses to the environment or to each other (demographic equivalence). These three viewpoints or paradigms make different predictions for community composition and species co-occurrence patterns over succession. If deterministic processes dominate (Clementsian model), we expect predictable species turnover as the system proceeds through succession with characteristic species composition

Manuscript received 14 July 2017; revised 27 September 2017; accepted 2 October 2017. Corresponding Editor: Rebecca L. McCulley.

⁴E-mail: inger.maaren@uib.no

emerging in different points in time (successional stages). A corollary is that the changes in community composition should be repeatable across different successions within the same general system (e.g., across different glacier forelands in the same region). Further, we can expect that the co-occurrence of species will be relatively stable, as species with similar ecological requirements will respond to the successional gradients in largely similar ways. If stochastic processes dominate (Gleasonian model), we can still have high species turnover over successional time that could be more or less repeatable across “replicate” successions based on priority effects and on how individual species’ niche requirements are fulfilled in different successional stages, but we would generally expect larger changes in species’ co-occurrence patterns between systems and over succession, as species react individualistically and may enter and be excluded from the community at different times, depending on an interplay between their niche requirements and chance events such as dispersal. The fastest change in both composition and co-occurrence is expected early in succession, when the community is not saturated. A neutral system, with species equivalence (Hubbellian model), such that species’ responses are driven by colonization-extinction dynamics and interactions rather than niche differences, can result in non-random species associations during succession (e.g., Ulrich et al. 2016), but we would generally expect low repeatability of both the specific community composition and of species co-occurrence patterns, both over successional time and between replicate successions.

Fire-prone ecosystems have repeatedly been used as model systems for testing ecological theory (Vitousek 2004, Bond and Keeley 2005, Mori 2011); in particular, the coastal heathlands of Western Europe is a classic system for studying successional processes (Watt 1947, Gimingham 1972, Miles 1979, Aerts and Heil 1993, Webb 1998). Heathland succession after fire is traditionally described by means of a Clementsian model, as a deterministic pathway based on structural change and species replacements from a “pioneer phase” after burning, through “building,” “mature,” and “degenerate” phases (Watt 1947, 1955, Gimingham 1972). Successional trajectories in these systems vary, depending on climate, local environmental conditions, management history, and in particular grazing levels (Hobbs and Gimingham 1984, Vandvik et al. 2005, Velle and Vandvik 2014, Velle et al. 2014). It is still unclear, however, to what extent the post-fire successions themselves, and in particular the temporal and spatial variation in successional patterns, is driven by stochastic or deterministic processes.

Grazing is of particular interest in the context of European coastal heathland ecology, as this ecosystem was created and maintained by humans over the past 5,000 years specifically to create grazing grounds for domestic herbivores, notably sheep and cattle (e.g., Gimingham 1972, Hobbs and Gimingham 1987, Webb 1998, reviewed in Vandvik et al. 2005).

Traditional heathland management thus involves the interplay of two kinds of disturbances; sporadic or rotational burning (a “pulse effect” that resets the ecosystem and starts successional dynamics) in combination with livestock grazing (a “press effect” that may deflect or modify successional dynamics). This has relevance for the level of determinism and stochasticity in heathlands successions. Grazing may act as a stochastic disturbance factor that slows down and adds stochasticity to succession without affecting the successional trajectory per se (Connell and Slatyer 1977, Hobbs 1996, Veblen and Young 2010). Grazing may also lead to alternative successional trajectories (Vandvik et al. 2005, Hidding et al. 2013), and as outlined above, this may result both from stochastic and from deterministic processes.

From an applied point of view, studies of the role of fire and grazing in affecting the biodiversity, ecology, ecosystem functioning, ecosystem service delivery, and evolutionary processes within heathland ecosystems feeds into the current debate on heathland and more generally upland and coastal ecosystem management in Europe (Davies et al. 2016), as well as related debates globally. Understanding successional processes can enable us to address and suggest mitigation measures for ecosystem change and degradation, and the study of ecological succession is therefore more relevant than ever (Foley et al. 2005).

Here, we examine patterns in community composition and species co-occurrence change over succession after management fires in coastal heathlands under different grazing regimes. We study vascular plant and bryophyte communities as the latter constitute a large fraction of the plant species pool and biomass in humid northern systems (Klanderud et al. 2015, Mateo et al. 2016), represent a physiological contrast to vascular plants and, therefore, are assumed to respond differently to environmental change (Grime et al. 1990, Proctor 1990), and are generally less well-studied in the successional literature (but see Clément and Touffet 1990, Maltby et al. 1990, Lee et al. 2013, Saure et al. 2014).

This study aims to assess empirically the role of stochastic vs. deterministic processes structuring bryophyte and vascular plant communities over post-fire succession in grazed and ungrazed seminatural heathlands. We use multivariate ordinations to assess the determinism in community assembly, which we measure as the predictability of species composition across replicate successions sequences in the landscape. We use co-occurrence analysis to assess to what extent species’ entry and exclusion from the communities are driven by their niche requirements (resulting in stable patterns of co-occurrence), vs. chance events, such as dispersal and random extinction, which will result in species entering and leaving communities independently of each other, both over time and across replicate successions (resulting in unstable patterns of co-occurrence). Based on the literature reviewed above we predict large community turnover but also high stochasticity in species co-occurrence immediately after

fire due to the combined effect of strong selective pressures and unsaturated communities, and lower community turnover and more deterministic co-occurrences later in succession as selective pressures decrease and communities saturate. We predict that grazing will deflect succession and result in predictable changes in community composition, due to species niche responses to grazing, but also that grazed systems will have higher change in species co-occurrences due to more pronounced stochasticity in grazed than in ungrazed vegetation. Finally, we predict that bryophytes, which are less adapted to grazing than vascular plants, will respond more strongly in terms of increased stochasticity in both community assembly and species co-occurrences in grazed systems relative to vascular plants.

METHODS

Study system and area

The coastal heathlands of northwestern Europe developed over the past 5,000 years by humans using fire to create year-round grazing pastures for free-ranging sheep and livestock (reviewed in Vandvik et al. 2014). They have since been maintained by domestic and wild ungulates, burning, turf-cutting, and/or heather and bracken harvesting (Gimingham 1972, Webb 1998). Over the past 50 years, traditional management has gradually declined, resulting in reforestation and heathlands are now classified as greatly endangered (EC Habitats Directive 92/43/EEC, Fremstad and Moen 2001, Lindgaard and Henriksen 2011).

Traditionally managed landscapes, such as heathlands, are useful experimental systems for ecology in that they provide opportunities for large-scale manipulations of successional trajectories (Young et al. 2001). The relatively short time scales in heathland successions (decadal scales) allow temporal successional studies, which can complement the chronosequence studies that dominate successional literature. This is important given the challenges associated with space-for-time substitutions in ecological research (Johnson and Miyanishi 2008).

Our study site is located at the island of Lurekalven (60°42' N, 5°5' E), situated in a fjord approximately 20 km inland from the Norwegian west coast. The climate is oceanic with January and July mean temperatures of 2°C and 12°C, respectively, a long growing season (~220 d above 5°C), and abundant precipitation (1,600 mm/yr.; data available online).⁵ The area has Pre-Cambrian bedrocks and soil pH ranges from 4.3 to 5.3 (Aarrestad and Vandvik 2000, www.ngu.no). The island is primarily covered by relatively species poor *Calluna* heath, with mires and *Salix* shrubs in the wetter parts and mixed grass-heaths on more nutrient-rich soils. Topography is a major source of local environmental variability; dry heath occurs on shallow soils on ridges

or in south-facing slopes, whereas moist heath occurs on deeper soils in north-facing slopes or in convex, poorly drained areas. The island is grazed year round by sheep; with an overall grazing pressure of ~1 sheep·ha⁻¹·yr⁻¹ (The Heathland Center at Lygra).

Experimental design and vegetation sampling

To create a no-grazing treatment, one part of the island was fenced off in 1993. Sheep of the Old Norse breed was restricted to one side (stocking density; ~1 sheep·ha⁻¹·yr⁻¹). On each side of the fence, six experimental blocks (~100 m² each), were placed in mature to degenerate phase *Calluna* heath (Gimingham 1972), to sample the range of heathland habitats (dry, intermediate, and moist heath; two replicate blocks in each habitat × grazing regime). Within each block, five 1-m² plots were placed in random positions and permanently marked with metal tubes. For all bryophyte and vascular plant species, frequency of occurrence (0–16) was recorded in 16 contiguous 0.25 × 0.25 m subplots and the percentage cover was visually estimated for the whole plot. The baseline survey was conducted in July/August 1993, and all 12 blocks were burned in April 1994. The plots were re-analysed in July/August each year between 1994 and 1998, and then again in 2003 and 2005 (when the vegetation reached the mature phase sensu Gimingham 1972), constituting seven sample years over the 13-year study period. Species that were difficult to separate consistently in the field (particularly difficult bryophyte taxa) were amalgamated at higher taxonomic levels. Species nomenclature follows the Norwegian Biodiversity Information Centre (available online).⁶ For information on species occurrences and taxonomy, see Appendix S1.

Data analyses

To visualize abundance and biomass build-up over time in the grazed and ungrazed successions, we plotted the sum of covers over time for five functional plant groups; trees and shrubs, dwarf-shrubs, forbs and ferns, graminoids, and bryophytes. For all subsequent analyses, the species composition was analysed in the full data set and split into separate data sets for bryophytes and vascular plants, and for the grazed and ungrazed area, as necessary to address specific research questions and predictions.

To assess the predictability of the trends in species composition across the 12 replicate post-fire successions, we used redundancy analysis (RDA; ter Braak 1986). Independent variables used were the interactive effects of factors representing grazing and time (grazing × year). The dependent variables were species cover, which were log-transformed (log[x + 1]) before analysis. Preliminary ordinations enabled an evaluation of the experimental setup; there was no significant overall differences between

⁵ www.met.no/en

⁶ www.biodiversity.no

grazed and ungrazed areas before the experiment was initiated in 1994 (1993 census, $P = 0.318$), indicating that the sampling regime was successful in selecting the same range of heathland habitats under the two grazing treatments (see Vandvik et al. [2005] for further details).

To quantify changes in species' co-occurrence over time, we followed the approach of Kapfer et al. (2013) using the plot-level presence/absence data. For each species and census, we counted the number of plots in which that species co-occurred with each of the other species in the data set, and standardized this value by dividing with the total number of plots the target species occurred in at this particular census. The standardized co-occurrences with other species were then averaged to yield one average co-occurrence value for each species. This analysis was conducted separately for each year of study resulting in one co-occurrence value for each individual species and year. To obtain an estimate of the change in co-occurrence, the value of the older inventory (year n) was subtracted from the value calculated for the more recent inventory (year $n + 1$, or $n + x$). The resulting negative (positive) value in species co-occurrence change indicates that species co-occur less (more) often in the more recent inventory compared to the older one. For each plot, we calculated the average absolute value of change in species co-occurrence across all species to get an indication of the overall stability (or change) in co-occurrence: The greater the absolute change in species co-occurrence, the less stable the assemblages are between the years of comparison. In other words, high change values (low stability) indicate that the community is re-assembling with each species behaving individually between the years of comparison, whereas low change values (high stability) indicate that plant communities are relatively stable, with species shifts happening more or less in concert. Because we cannot know exactly how much of the observed species co-occurrence change between years is due to change occurring by chance (e.g., random movement of species within communities), we estimated a so-called "expected" change. For this purpose, we created a null model by randomizing all samples, with their observed species composition, between years of comparison. After all plots were re-assigned randomly across the various treatments and years of comparison, the new (randomized) data set was analysed in the same way as for the original (un-randomized) data set to generate "expected change." We ran 999 permutations of this null model and P -values were then calculated counting the number of times the observed change was greater than or equal to the expected change. Finally, observed changes were standardized by subtracting the expected changes from the observed, and dividing this value by the standard deviation.

To test to what extent variation in species richness between treatments or across the successional series affected the outcome of the co-occurrence analyses we ran sensitivity analyses. To do this we made 1,000 randomized data sets by randomly selecting plots from the total pool of plots (over all times and treatments). The number of

plots selected corresponds to the number of plots used in the analyses above (i.e., for the two time periods compared). Each of these data sets was treated as the observed data set. Selecting 1,000 randomized data sets as the observed data set gave a variation in the different richness estimates (i.e., total richness in the initial sample, total richness in the resample, average plot richness in both the original and the resample) similar to the variation observed along the gradients studied (Appendix S2). We subsequently performed the same analysis randomizing procedures on these new observed data sets as for the real observed data set (see detailed description above). Despite the high number of data points (1,000 from the permutations), we generally found a non-significant relationship between the number of species and the co-occurrence metric, and the variance that was explained by species richness was generally low. We therefore conclude that the co-occurrence analyses shown here are not sensitive to variation in species richness (for more details, see Appendix S2).

All statistical analyses were run in R, version 3.1.0 (R Core Team 2014) using the package *vegan* (Oksanen et al. 2013) for the ordination analyses.

RESULTS

The above ground vegetation cover decreases dramatically after fire, and recovers gradually over the following 13 years, with clear differences between functional groups and grazing regimes (Fig. 1; Appendix S3). Graminoids increase after fire and reach peak cover after 4 years, whereas forb cover is relatively unaffected. In contrast, dwarf shrubs and bryophytes, which dominate the pre-burn vegetation, are reduced by more than 90% after fire, and recover slowly to regain dominance with mean covers close to the pre-burn vegetation after nine years.

Repeatable community changes

There are clear and parallel post-fire successional trends in vascular plant species composition across the replicate fire blocks in both grazed and ungrazed heath (largely reflected along RDA axis 1, 5.26% variance, Fig. 2a). The overall community change is higher in the first two years after fire, when there is also a change in the direction of succession. There are also clear differences between grazed and ungrazed successions, both in species composition (reflected as an offset along RDA axis 2, 2.67% variance, Fig. 2a), and in successional dynamics, as the ungrazed successions start to revert back toward the pre-fire community composition after ~5 years, whereas the grazed successions do not.

In the bryophyte communities, clear parallel successional dynamics across the replicate successions are only evident in the ungrazed heaths, where community composition changes dramatically in the first year after fire, and then changes more slowly and gradually reverts back toward the pre-fire community composition (RDA axis 1; 5.41% variance, axis 2; 2.71% variance, Fig. 2b).

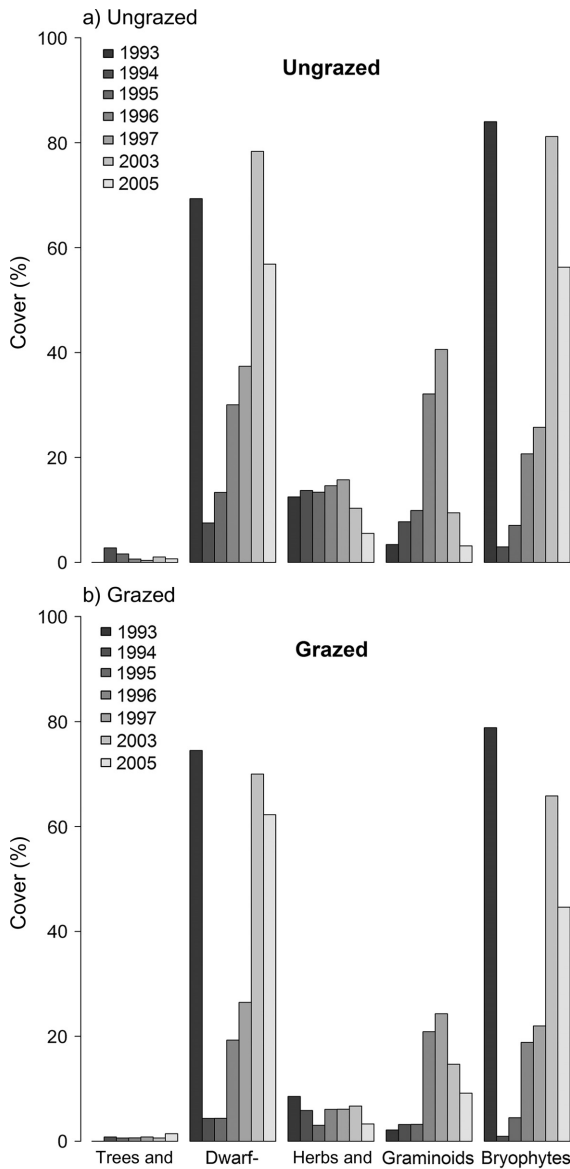


FIG. 1. Total mean cover of the five main functional groups of plants found in the heathlands of Western Norway before burning (1993) and over the course of the post-fire succession (up to 2005) in (a) ungrazed and (b) grazed vegetation.

In contrast, there does not seem to be any overall trend in the species composition over 13 years after fire across the grazed bryophyte communities. In addition to these striking differences in successional dynamics, grazed and ungrazed successions also differ in terms of bryophyte community composition, especially in late-successional stages (Fig. 2b).

Synchrony in species responses

We detected large and significant year-to-year changes in vascular plant species co-occurrences over the first two

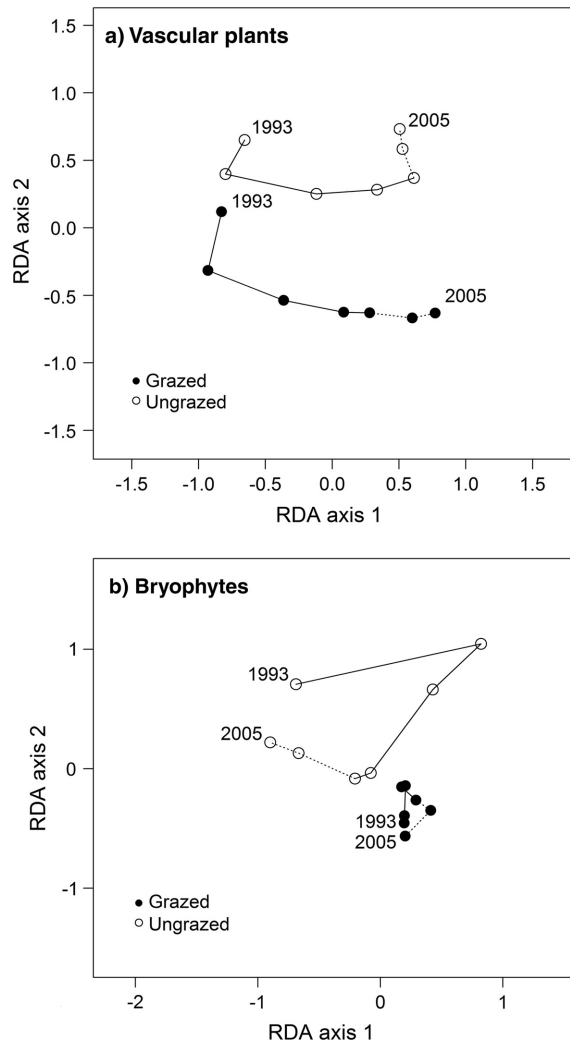


FIG. 2. Redundancy analysis (RDA) ordination plot of species frequency data for the (a) vascular plant and (b) bryophyte communities during the post-fire successions at Lygra, Western Norway. Solid and open circles indicate centroids of all grazed and ungrazed plots, respectively, for each of the seven sampled years of the 13-years post-fire study. Species frequency data were log transformed before analysis. Solid lines show single-year transitions (1993–1997) and dashed lines multi-year transitions (1997–2003/2003–2005).

years after fire, followed by a decrease in change rates in later-successional stages (year-to-year change in co-occurrence is not significant from 1997 and onward, Fig. 3a). This pattern is stronger in the ungrazed successions. When we compare each sampled year of the post-fire succession to the pre-fire vegetation state (Fig. 3b), we find that the significant changes in vascular plant species co-occurrences is retained throughout the 13 years of succession, but with maximum change relative to the pre-fire condition in the middle of the succession. As in the year-to-year analyses, changes are more marked in the ungrazed vegetation (in grazed vegetation, it is significant only in 1997 and 2003). The total vascular

plant data set (grazed + ungrazed) has much larger changes in co-occurrence throughout the succession than either the grazed or the ungrazed (Fig. 3b), suggesting that species assembling differently so that grazed and ungrazed successional communities are becoming more dissimilar with time.

For bryophytes the change in co-occurrence is consistently high, especially in the grazed heaths, both from year to year (Fig. 3a) and when comparing each year to the pre-fire state (Fig. 3b). Changes in co-occurrence in the total bryophyte community were of similar magnitude

to the change within the grazed or ungrazed areas (Fig. 3b), suggesting that there is no increasing dissimilarity in species' co-occurrences between the grazed and ungrazed bryophyte communities over time.

DISCUSSION

Changes in species co-occurrence patterns over successional time indicate that both deterministic and stochastic processes play important roles in controlling the species assembly and succession of the post-fire heathland

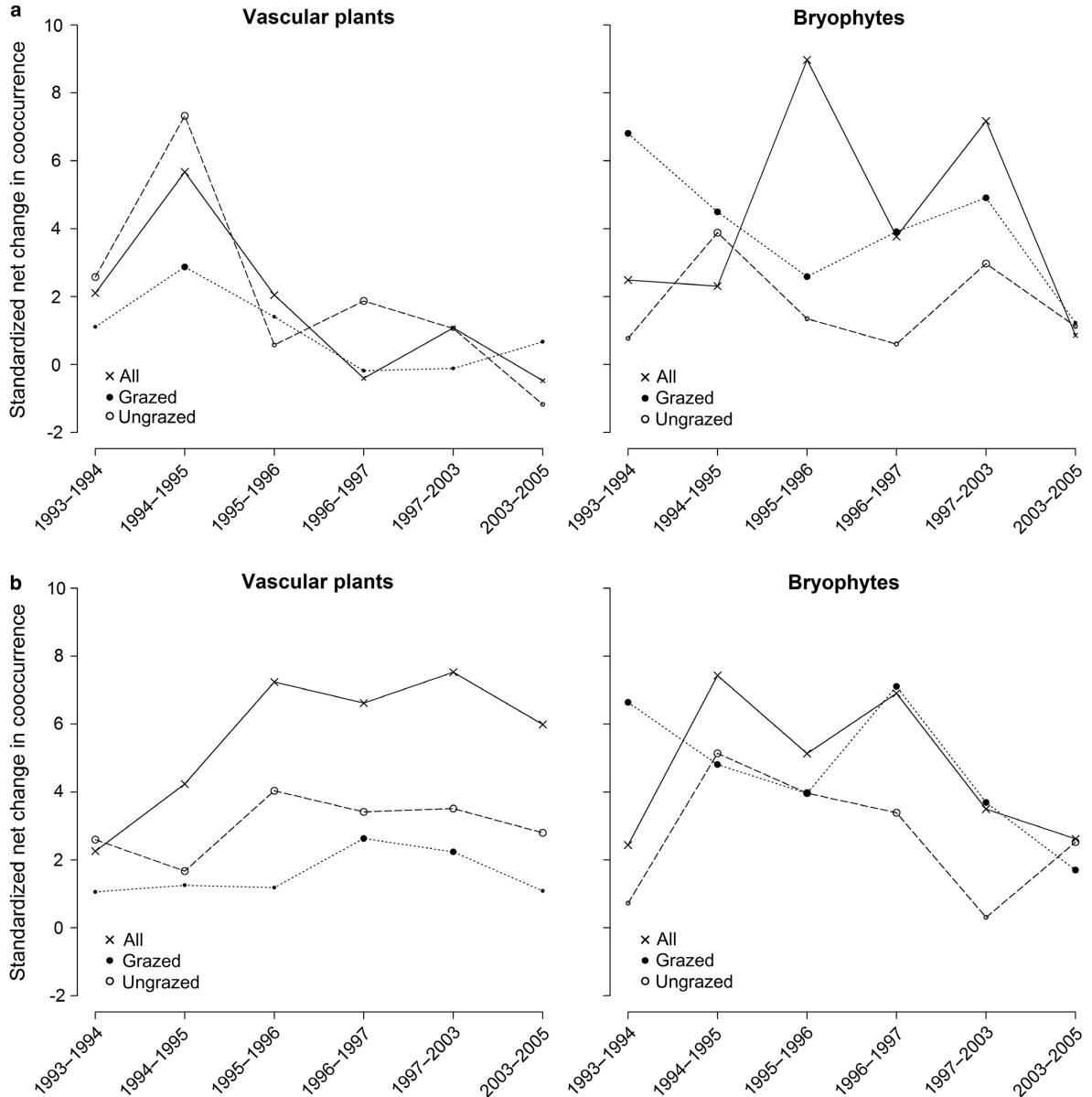


FIG. 3. Standardized net changes ($[\text{observed} - \text{expected}]/\text{SD}$) in species co-occurrences (a) from each census to the next and (b) relative to the pre-fire census for vascular plants and bryophytes over a post-fire succession in coastal heathlands in Western Norway. For each grazing treatment and census, large symbols signify significant change in co-occurrence and small symbols non-significant change.

community, but their relative importance varies over time, between plant functional groups, and also in response to other management practices, as in this case livestock grazing: Immediately after fire, we see large community turnover but also high stochasticity in species co-occurrence due to the combined effects of strong selective pressures and unsaturated communities, and lower community turnover and more deterministic co-occurrences later in succession as selective pressures decrease and communities saturate. Grazing deflects succession and results in predictable changes in community composition, due to species niche responses to grazing, and grazed systems show greater change in species co-occurrences and more pronounced stochasticity in grazed than in ungrazed vegetation. Bryophytes, which are less adapted to grazing than vascular plants, show higher stochasticity in both community assembly and species co-occurrences in grazed systems in comparison to the vascular plants.

High community turnover and high stochasticity in species co-occurrences right after fire

In the first growing season after the heathland burning and the following year (1994 and 1995), all species are impacted severely by the massive disturbance event. The environment changes from a typically homogenous mature *Calluna*-dominated stand to a heterogeneous microsite mosaic. The newly burned areas are colonized by species dispersing in from the surrounding areas or that have survived the fire in the propagule bank, or that re-sprout from roots or surviving plants. As indicated by the low stability of co-occurrences between 1994 and 1995 (Fig. 3a), random processes largely determine which specific species, especially for the vascular plants, and in which specific order they colonize the different burns. The ordination analyses (Fig. 2) indicate that there are also repeatable, across replicate sites, changes in species composition, suggesting that deterministic species sorting processes also operate on the total species pool at this stage.

Later in succession, the overall community change rates across successions decline, but the underlying processes driving the changes are more deterministic, as indicated by the decreasing co-occurrence change rates. Thus, the ordination and co-occurrence analyses combined indicate that the drivers of community compositional change over succession shifts from largely stochastic processes early in succession toward more deterministic processes as the communities saturate over time (see Fig. 3). This concurs with the findings of several recent studies (e.g., Kahmen et al. 2002, Gravel et al. 2006, Adler et al. 2007, Chu et al. 2007, Harpole and Tilman 2007, Zaplata et al. 2013), revealing that both high and more gradual species turnover may operate within vascular plant communities, driving community dynamics and structuring species assemblages. In early succession, we see relatively large change rates, indicating species sorting and new constellations of species. Later, we see much lower change in co-occurrence (and low turnover), and we have stable communities over years. For

the bryophytes, we see a very different picture (see Fig. 3). In the grazed vegetation, we see low species turnover and at the same time high co-occurrence change rates. This is compatible with a system where neutral dynamics and stochastic processes dominate. There is no indication of this changing throughout the succession, even if vegetation cover regains its stature. In contrast, in the ungrazed vegetation bryophytes behave very differently. Here, greater predictability in community composition change across the replicate burns and simultaneously high change in co-occurrence rates early on, which peak and thereafter decline later in succession, suggests successional community change is driven primarily by stochastic processes early in succession and by deterministic niche-based species sorting in later successional stages, similar to what we found in the vascular plant community. Such sorting processes can be direct, driven by environmental factors (Zaplata et al. 2013); and indirect, driven by species interactions (Olsen et al. 2016). As we do not have environmental data for every sample and year (due to economic constraints), we cannot formally attribute these deterministic changes to specific environmental factors. The most robust way of attributing species and community responses to specific direct or indirect drivers is through manipulative experiments (e.g., Olsen et al. 2016), but observational methods such as gradient studies or “space-for time” approaches are also possible (Zaplata et al. 2013, Klanderud et al. 2015, Ulrich et al. 2016).

Stochastic processes are more pronounced in grazed than in ungrazed successions

Herbivory is a major driver of vegetation dynamics and a critical component of land-use impacts worldwide (Asner et al. 2004). The heathland literature debates the role of grazing as a factor that delays or deflects succession (see Vandvik et al. 2005), and its impacts has consequences for heathland management, particularly in regions with rare or threatened species. We find that the vegetation rearranges faster and the processes are more deterministic in ungrazed sites, while slower and more chaotic/stochastic in grazed sites. For vascular plants, we find deterministic turnover both within and between grazing regimes, showing that grazing deflects succession. However, the grazed sites are still more influenced by chance events, illustrated by the high co-occurrence change rates here, due to disturbance caused by the grazers (destroying vegetation by grazing, browsing, and trampling, creating new microhabitats for species, and soil erosion), causing randomness. In contrast, in the ungrazed sites, the re-arrangement of species is more predictable, resulting in more or less the same species composition as before the fire, and in congruence with Azeria et al. (2011) that found non-random species co-occurrences to correspond to some fundamental ecological mechanisms that act during succession (e.g., inhibitive or competitive interactions), or to specific management regimes (e.g., livestock grazing systems). In our case, the ungrazed heathlands are driven by high species turnover, mainly as a result of competition during the post-fire

succession where the relatively rapid regeneration of the *Calluna* canopy shades out photophilous species. We also see more re-shuffling (higher change rates) in the ungrazed vascular plant vegetation. Grazed heathlands, on the other hand, are more influenced by stochastic processes (low change rates), most likely driven by impacts of the grazing livestock, where sheep trampling and herbivory may create more heterogeneous micro-site conditions in the vegetation development. For bryophytes, grazing represents a stochastic factor that efficiently negates all species sorting, and we do not see the semi-stable system here, not even in the ungrazed vegetation. The hump in co-occurrence change between 1994 and 1995 (see Fig. 3) shows the stochastic aspect, and here the environmental heterogeneity is at its largest. Grazing is, therefore, an important structuring factor in the post-fire succession, partly determining which species establish, and later, become dominants.

Stochastic processes are more important for bryophyte than for vascular plant communities

For vascular plants, we see the largest change in co-occurrence over the first two years of the succession, with largest change in the ungrazed vegetation, possibly explained by stronger competition between plants in the ungrazed early post-fire vegetation, and after three years we still see a legacy effect of high species turnover. For the bryophytes we lack this initial sorting of neighbors, probably due to the high environmental heterogeneity in post-fire micro-site conditions and its implications for bryophyte growth and recovery. Bryophytes, in particular, are conducive to changes in micro-site conditions, and more so than vascular plants (Herben 1987). Fire consumes biomass unequally during management burns, creating heterogeneity in the post-fire heath with pockets of unburned heath, exposed soil, and patches of partially burned bryophyte cover (Vandvik et al. 2005, Måren and Vandvik 2009). Consequently, bryophytes in these patches are likely to re-colonize the nearby burned areas, with little, if any, change to species composition. In wetter heathlands, bryophyte growth may be more extensive as vascular plant re-colonization here is slow, as nicely illustrated by Letten et al. (2014) who found fire to prevent the competitive exclusion of early successional species by late successional ones in an Australian heathland.

In the ungrazed sites, the species composition clearly changes over the post-fire succession, reflecting species with less affinity to light ("forest species"), e.g., *Hylacomium splendens*, *Pleurozium schreberi*, and *Rhytidiadelphus loreus* (Appendix S4), caused by closure of the *Calluna* canopy. Grazed sites are characterized by the fire mosses *Ceratodon purpureus* and *Leptodontium flexifolium* and species of the genera *Pohlia* and *Bryum*, and the liverwort genera *Calyptogeia*, *Jungermannia*, and *Scapania*. These bryophytes are favored by a slower closing of the vegetation canopy, caused by livestock grazing and browsing (grazers that prefer to graze within newly

burned sites), and by the creation of new microhabitats by trampling and soil disturbance/erosion by the same grazers.

CONCLUSIONS

We observed change in community assembly processes over successional time, where variation was dependent on grazing regime and plant functional group; chance and individualistic species responses early in succession gave way to more niche-driven dynamics in later successional stages. Grazing reduced predictability in both successional trends and species-level dynamics, especially for bryophytes. We see imprints of all the three successional paradigms considered here. The vascular plant community showed highly deterministic community compositional change early in succession that later stabilized. Co-occurrence patterns point to largely stochastic species-level dynamics early on, which give way to more deterministic species replacements after the first few years. Grazed and ungrazed successions were similar, but the early stage stochasticity was higher in ungrazed areas. Bryophyte communities in ungrazed successions resembled vascular plant communities. In contrast, bryophytes in grazed successions showed consistently high stochasticity and low determinism in both community composition and species co-occurrence.

Anthropogenic systems present a dilemma for management, as disturbances are integral parts of the very systems that we want to conserve, but simultaneously they may facilitate unintended change, e.g., by instigating loss of habitat/species, or by opening up regeneration niches for invasive species (Western 2001, Collins and Smith 2006, Kremen and Miles 2012). Despite extensive development of successional theory, few empirical studies have evaluated whether existing models are applicable to anthropogenic landscapes (Bhaskar et al. 2014). To quote Clements (1949), "In short, as an instrument for the control of the entire range of human uses of vegetation and the land, succession is wholly unrivalled." In this sense, understanding successional dynamics is especially pertinent to sustainable land management and future food production. Here, we have used anthropogenic heathlands to explore assembly processes during succession. Our results emphasize the need for a better understanding of the complex assembly of ecological communities during succession, where explaining the processes affecting coexistence is at the heart of the debate (Adler et al. 2007, Harpole and Tilman 2007).

ACKNOWLEDGMENTS

We thank Peter Emil Kaland who initiated the project, Sigrunn Dommarsnes, Vibeke Husby, Kristine Ekelund, Fride Høistad Schei, and Håvard Laukland for fieldwork assistance, Arne Frisvoll, Bjørn Moe, and Einar Heegaard for bryophyte identifications, and NINA, Grolle Olsens Legat, the Research Council of Norway (grant 194051) and Bergen Myrdrkningsforeningsfond for financial support. There is no conflict of interest concerning this paper.

LITERATURE CITED

- Aarrestad, P. A., and V. Vandvik. 2000. Vegetation change in west-Norwegian coastal heathland – effects of the management methods fire and sheep grazing in rehabilitation of old heathland on Lurekalven in Hordaland. NINA Report 044:1–60.
- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Aerts, R., and G. W. Heil. 1993. *Geobotany 20. Heathland: patterns and processes in a changing environment*. Kluwer Academic, London.
- Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29:261–299.
- Azeria, E. T., M. Bouchard, D. Pothier, D. Fortin, and C. Hébert. 2011. Using biodiversity deconstruction to disentangle assembly and diversity dynamics of understorey plants along post-fire succession in boreal forest. *Global Ecology and Biogeography* 20:119–133.
- Bhaskar, R., T. E. Dawson, and P. Balvanera. 2014. Community assembly and functional diversity along succession post-management. *Functional Ecology* 28:1256–1265.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global herbivore: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20:387–394.
- Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391.
- Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B* 366:2351–2363.
- Chu, C., Y. Wang, G. Du, F. T. Maestre, Y. Luo, and G. Wang. 2007. On the balance between niche and neutral processes as drivers of community structure along a successional gradient: Insights from alpine and sub-alpine meadow communities. *Annals of Botany* 100:807–812.
- Clément, B., and J. Touffet. 1990. Plant strategies and secondary succession on Brittany heathlands after severe fire. *Journal of Vegetation Science* 1:195–202.
- Clements, F. E. 1916. *Plant succession, an analysis of the development of vegetation*. Publication 242. Carnegie Institution of Washington, Washington, D.C., USA.
- Clements, F. E. 1949. *Dynamics of vegetation*. H. W. Wilson, New York, New York, USA.
- Collins, S. L., and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tall-grass prairie. *Ecology* 87:2058–2067.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Davies, G. M., et al. 2016. The role of fire in UK peatland and moorland management: the need for informed, unbiased debate. *Philosophical Transactions of the Royal Society B* 371:20150342.
- Drake, J. A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147:213–233.
- Eliot, C. 2007. Method and metaphysics in Clements's and Gleason's ecological explanations. *Studies in History and Philosophy of Biological and Biomedical Sciences* 38:85–109.
- Foley, J. A., et al. 2005. Global consequences of land-use. *Science* 309:570–574.
- Fremstad, E., and A. Moen, editors. 2001. *Threatened vegetation types in Norway*. NTNU Vitenskapsmuseet Rapport Botanisk Serie 2001–4:1–231.
- Gimingham, C. H. 1972. *Ecology of heathlands*. Chapman and Hall, London, UK.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- Glenn-Levin, D. C., R. K. Peet, and T. T. Veblen, editors. 1992. *Plant succession. Theory and prediction*. Chapman and Hall, London, UK.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399–409.
- Grime, J. P., E. R. Rincon, and B. E. Wickerson. 1990. Bryophytes and plant strategy theory. *Botanical Journal of the Linnean Society* 104:175–186.
- Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446:791–793.
- Helsen, K., M. Hermy, and O. Honnay. 2013. Spatial isolation slows down directional plant functional group assembly in restored semi-natural grasslands. *Journal of Applied Ecology* 50:404–413.
- Herben, T. 1987. Bryophytes in grassland vegetation sample plots: what is their correlation with vascular plants. *Folia Geobotanica et Phytotaxonomica* 22:35–41.
- Hester, A. J., I. J. Gordon, G. J. Baillie, and E. Tappin. 1999. Foraging behaviour of sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology* 36:133–146.
- Hidding, B., J.-P. Tremblay, and S. D. Côté. 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology* 94:2852–2860.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- Hobbs, R. J., and C. H. Gimingham. 1984. Studies on fire in Scottish heathland communities. II. Post-fire vegetation development. *Journal of Ecology* 72:585–610.
- Hobbs, R. J., and C. H. Gimingham. 1987. Vegetation, fire and herbivore interactions in heathland. *Advances in Ecological Research* 16:87–173.
- Hobbs, R. J., A. Jentsch, and V. M. Temperton. 2007. Restoration as a process of assembly and succession mediated by disturbance. Pages 150–167 in L. R. Walker, J. Walker, and R. J. Hobbs, editors. *Linking restoration and ecological succession*. Springer Series on Environmental Management, New York, New York, USA.
- Hubbell, S. P. 2001. *The united neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* 11:419–431.
- Kahmen, S., P. Poschold, and K.-F. Schreiber. 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* 104:319–328.
- Kapfer, J., H. J. B. Birks, V. A. Felde, K. Klanderud, T. Martinessen, L. C. Ross, F. H. Schei, R. Virtanen, and J.-A. Grytnes. 2013. Long-term vegetation stability in northern Europe as assessed by changes in species co-occurrences. *Plant Ecology and Diversity* 6:289–302.
- Klanderud, K., V. Vandvik, and D. Goldberg. 2015. The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS ONE* 10:e0130205.
- Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and Society* 17:40.
- Kreyling, J., A. Jentsch, and C. Beierkuhnlein. 2011. Stochastic trajectories of succession initiated by extreme climatic events. *Ecology Letters* 14:758–764.

- Lee, H., J. G. Alday, R. J. Rose, J. O'Reilly, and R. H. Marrs. 2013. Long-term effects of rotational prescribed burning and low-intensity sheep-grazing on blanket-bog plant communities. *Journal of Applied Ecology* 50:625–635.
- Letten, A. D., D. A. Keith, and M. G. Tozer. 2014. Phylogenetic and functional dissimilarity does not increase during temporal heathland succession. *Proceedings of the Royal Society B* 281:1797.
- Lindgaard, A., and S. Henriksen. 2011. The 2011 Norwegian red list for ecosystems and habitat types. Norwegian Biodiversity Information Centre, Trondheim, Norway.
- Maltby, E., C. J. Legg, and M. C. F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. *Journal of Ecology* 78:490–518.
- Måren, I., and V. Vandvik. 2009. Fire and regeneration: the role of seed banks in the dynamics of northern heathlands. *Journal of Vegetation Science* 20:871–888.
- Mateo, R. G., et al. 2016. The mossy north: an inverse latitudinal diversity gradient in European bryophytes. *Scientific Reports*. <https://doi.org/10.1038/srep25546>
- Miles, J. 1979. *Vegetation dynamics*. Chapman and Hall, London, UK.
- Mori, A. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. *Journal of Applied Ecology* 48:280–292.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan: community ecology package*. R package version 2.0-6. <http://CRAN.R-project.org/package=vegan>
- Olsen, S., J. P. Töpper, O. Skarpaas, V. Vandvik, and K. Klanderud. 2016. From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology* 22:1915–1926.
- Pickett, S. T. A., and M. L. Cadenasso. 2005. *Vegetation dynamics*. Pages 172–198 in E. van der Maarel, editor. *Vegetation ecology*. Blackwell Science, Malden, Massachusetts, USA.
- Pickett, S. T. A., M. L. Cadenasso, and S. J. Meiners. 2008. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science* 12:9–21.
- Proctor, M. C. F. 1990. The physiological basis of bryophyte production. *Botanical Journal of the Linnean Society* 104:61–77.
- R Core Team. 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ravel, V., F. Munoz, V. Pons, A. Renaux, A. Martin, and J. D. Thompson. 2013. Changing assembly processes during a primary succession of plant communities on Mediterranean road cuts. *Journal of Plant Ecology* 6:19–28.
- Saure, H. I., V. Vandvik, K. Hassel, and O. R. Vetaas. 2014. Do vascular plants and bryophytes respond differently to coniferous invasion of coastal heathlands? *Biological Invasions* 16:775–791.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.
- Ulrich, W., M. K. Zaplata, S. Winter, W. Schaaf, A. Fischer, S. Soliveres, and N. J. Gotelli. 2016. Species interactions and random dispersal rather than habitat filtering drive community assembly during early plant succession. *Oikos* 125:698–707.
- Vandvik, V., E. Heegaard, I. Måren, and P. Aarrestad. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post fire succession in heathlands. *Journal of Applied Ecology* 42:139–149.
- Vandvik, V., J. P. Töpper, Z. Cook, M. I. Daws, E. Heegaard, I. E. Måren, and L. G. Velle. 2014. Management-driven evolution in a domesticated ecosystem. *Biology Letters* 10: 20131082.
- Veblen, K. E., and T. P. Young. 2010. Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *Journal of Ecology* 98:993–1001.
- Velle, L. G., and V. Vandvik. 2014. Succession after prescribed burning in coastal Calluna heathlands along a 340-km latitudinal gradient. *Journal of Vegetation Science* 25:546–558.
- Velle, L. G., L. S. Nilsen, A. Norderhaug, and V. Vandvik. 2014. Does prescribed burning result in biotic homogenization of coastal heathlands? *Global Change Biology* 20:1429–1440.
- Vitousek, P. M. 2004. *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton University Press, Princeton, New Jersey, USA.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1–22.
- Watt, A. S. 1955. Bracken versus heather: a study in plant sociology. *Journal of Ecology* 43:490–506.
- Webb, N. R. 1998. The traditional management of the European heathlands. *Journal of Applied Ecology* 35:987–990.
- Western, D. 2001. Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences USA* 98:5458–5465.
- Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly. Comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration* 19:5–19.
- Zaplata, M. K., S. Winter, A. Fisher, J. Kollmann, and W. Ulrich. 2013. Species-driven phases and increasing structure in early-successional plant communities. *American Naturalist* 181:E17–E27.
- Zhou, J.-Z., et al. 2014. Stochasticity, succession, and environmental perturbations in a fluidic ecosystem. *Proceedings of the National Academy of Sciences USA* 111:836–845.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2052/supinfo>