

Experimental evidence for herbivore limitation of the treeline

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Abstract. The treeline ecotone divides forest from open alpine or arctic vegetation states. Treelines are generally perceived to be temperature limited. The role of herbivores in limiting the treeline is more controversial, as experimental evidence from relevant large scales is lacking. Here we quantify the impact of different experimentally controlled herbivore densities on the recruitment and survival of birch *Betula pubescens tortuosa* along an altitudinal gradient in the mountains of southern Norway. After eight years of summer grazing in large-scale enclosures at densities of 0, 25, and 80 sheep/km², birch recruited within the whole altitudinal range of ungrazed enclosures, but recruitment was rarer in enclosures with low-density sheep and was largely limited to within the treeline in enclosures with high-density sheep. In contrast, the distribution of saplings (birch older than the experiment) did not differ between grazing treatments, suggesting that grazing sheep primarily limit the establishment of new tree recruits rather than decrease the survival of existing individuals. This study provides direct experimental evidence that herbivores can limit the treeline below its potential at the landscape scale and even at low herbivore densities in this climatic zone. Land use changes should thus be considered in addition to climatic changes as potential drivers of ecotone shifts.

Key words: *Betula pubescens tortuosa*; browsing; ecotone shifts; encroachment; grazing; mountain birch; southern Scandes, Norway; sheep; treeline limitation; vegetation state change.

INTRODUCTION

Studies at the range margins of species provide insights into processes that are fundamental to species' responses to environmental changes (Holt and Kleitt 2005). The treeline is a particularly apparent range margin, showing a clear ecological distinction between the forest and alpine or arctic vegetation states. Forests and arctic or alpine ecosystems differ markedly in terms of ecosystem function; thus, changes in the position of the altitudinal and latitudinal treelines will have huge implications for biotic communities, landscapes, and land use (e.g., Hofgaard and Wilmann 2002, Baker and Moseley 2007, Hester and Brooker 2007). Here we use the term "forest line" as the upper limit of closed-canopy forest, "treeline" as the limit of groups of mature individuals, and "tree species line" as the limit of individuals of any size, whereas the "treeline ecotone" spans the zone from the forest line to tree species line (Korner and Paulsen 2004).

Climate, and in particular temperature, is perceived to be the main control over the position of the treeline at

larger scales (e.g., Korner and Paulsen 2004, Kullman and Oberg 2009). A recent global meta-analysis of 166 treelines found that over half had advanced in altitude since AD 1900 in relation to warming over the past century (Harsch et al. 2009). However, 48% of treelines had not advanced since 1900 (Harsch et al. 2009). Although temperature limitation is at the forefront of research on the limitation of tree species and treelines, other factors have also been linked with limitation of the treeline, including land use and herbivory (Hofgaard 1997, Cairns and Moen 2004, Hester and Brooker 2007). Theoretical models of treeline limitation by herbivores have been proposed (Cairns and Moen 2004) and comparative studies have suggested that herbivores may either limit tree establishment (Cairns and Moen 2004, Dalen and Hofgaard 2005) or promote tree establishment (Tømmervik et al. 2009) at the forest–alpine ecotone. However, comparative studies have struggled to disentangle the effects of land use or herbivory from climate (Gehrig-Fasel et al. 2007, Hofgaard et al. 2009). Thus, to understand the impact of herbivores on treeline dynamics and to ascertain whether changes in grazing practice could be responsible for shifts between these vegetation states, experimental studies are required.

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In many areas of Europe, land use has changed over the past decades with altering agricultural regimes and decreasing mowing frequency and fuel wood collection (Olsson et al. 2000, Gehrig-Fasel et al. 2007, Tasser et al. 2007). In particular, the extensive grazing of livestock in upland pastures has decreased with agricultural intensification (e.g., Dallimer et al. 2009). This change in land use could lead to encroachment of woody plants into alpine communities and a vegetation state transition from open landscape to forest (Hofgaard 1997, Tasser et al. 2007). The combined impact of a warming climate and decreasing livestock densities could result in the loss of large areas of alpine regions. Indeed, recent small-scale enclosure studies have documented a potential for herbivores to prevent climate-driven shrub encroachment within tundra plant communities (Post and Pedersen 2008, Olofsson et al. 2009). However, these studies did not have direct control over herbivore density, and due to their limited area it is difficult to extrapolate the findings to the more relevant landscape scale.

In this study, we used a replicated landscape-scale grazing enclosure experiment to investigate the impact of three densities of sheep grazing during the summer on the distribution and recruitment of mountain birch (*Betula pubescens tortuosa*) above the forest line in the southern Scandes Mountains of Norway. We predicted that birch recruitment would vary with altitude, sheep density, and productivity. We hypothesised that low herbivore densities would allow increases in tree establishment at and above the treeline, whereas high herbivore densities would decrease tree establishment. Cairns and Moen (2004) proposed that the response of the treeline to herbivory will depend on the relative preference of herbivores for the treeline species in comparison to the field vegetation, the tolerance of the treeline species and field layer to herbivore presence, and the requirement of recruiting birch for the disturbance and limitation of competition caused by herbivores. Thus we also expected the response of the treeline to herbivore density to be habitat specific.

METHODS

Experimental setup

The experimental site is in the municipality of Hol, Norway (7°55' to 8°00' E, 60°40' to 60°45' N). In 2001, a 2.7-km² enclosure was erected and split into 9 sub-enclosures with an average area of 0.3 km² (Austrheim et al. 2008). Three treatments were applied within the sub-enclosures in a block design. The treatments were: ungrazed (no sheep), low sheep density (25 sheep/km²), and high sheep density (80 sheep/km²). A botanical survey and assessment of the grazing value of the site vegetation for sheep provided the basis for choosing treatments of 25 and 80 sheep/km² as low and high densities, respectively (Rekdal 2001). These density

levels are within the typical range for Norwegian alpine summer pastures. Grazing frequencies of herbs indicate that these sheep densities yield low and moderate grazing (Evju et al. 2006). The sheep were of the “Norwegian white” breed (also known as “Dala”) and were grazed within the enclosures every summer from 2002, typically from late June to early September in accordance with usual summer grazing practice in this area (Møbæk et al. 2009). Prior to erecting the enclosures, the density of sheep grazed in the region is estimated to have been low (around 10 sheep/km²).

The experimental enclosure was situated on a south-facing slope, ranging from 1050 to 1320 m above sea level (a.s.l.). The vegetation at the site is mainly composed of dwarf shrub and lichen heaths, with *Salix* thickets, meadows, and snowbeds interspersed (for a detailed description of the site vegetation, see Austrheim et al. 2008). The vegetation communities were grouped according to productivity (Møbæk et al. 2009): low-productivity communities were lichen heaths, moss snowbeds, bogs, fens, and stone polygon land. Graminoid snowbeds and dwarf shrub heaths were classed as medium productivity, and the high-productivity habitat consisted of tall and low herb meadow communities. The mean annual and summer (June–August) temperatures during the period 2002–2008 were –0.7°C and 8.8°C, and the long-term (1961–1990) annual and summer temperatures were –1.6°C and 7.9°C (data provided by the Norwegian Meteorological Institute, interpolated from nearby weather stations).

The treeline-forming species in this area is the mountain birch (*Betula pubescens tortuosa*), although limited numbers of *Sorbus aucuparia*, *Populus tremula*, *Pinus sylvestris*, and *Picea abies* are also found in the enclosures. The lower part of the enclosure is above the present forest line, which is around 1000 to 1050 m a.s.l. at this location. The treeline is within the central and eastern part of the enclosures, at an altitude of between 1150 and 1200 m (Fig. 1), while the tree species limit extends upslope of the experiment; birch individuals are found at altitudes of up to 1315 m in and around the enclosure. The observed treeline and forest line at this site are likely to have been suppressed below their climatic potential by historical land use and high grazing pressure, in common with other areas of Norway (Hofgaard 1997, Olsson et al. 2000).

Sampling

This study focused on birch, the dominant and treeline-forming tree species at the experimental site. Birch were sampled along line transects during August 2009. Twenty-three transects were regularly positioned across the enclosures running on the east–west axis. These were sampled in a stratified random order, with a random direction. Transect lines were walked using the course function on a handheld GPS device. The total

transect length was 42 km. Birch were searched for and recorded up to 5 m on either side of the transect centerline. Birch were recorded as being either immature (<2 m tall) or mature (>2 m tall); this is consistent with other birch treeline studies (e.g., Hofgaard et al. 2009). The position of every birch individual was recorded by GPS. In addition, the vertical height (ground level to highest point without stretching birch) and basal stem diameter of all immature birch individuals were recorded.

Immature birch were further classified after sampling; birch recruits were defined as those with a stem diameter of ≤ 15 mm, which was estimated to be the maximum size obtainable for a birch recruiting within the length of the experiment (9 years; the last year of nonexperimental sheep grazing was 2001). Immature birches with a stem diameter > 15 mm were estimated to have recruited prior to the start of grazing treatment and were classified as saplings. This threshold was based on ring-count aging of 100 immature birch destructively harvested from immediately outside the enclosure (ring-count method following Hofgaard et al. 2009). These individuals were sampled from all sides of the enclosure, providing a range of altitude and vegetation types representative of those within the enclosures. The maximum stem diameter of a 9-year-old birch sampled from outside the enclosure was 14 mm. Altitude was not a significant covariate in the relationship between stem diameter and age.

Statistical analyses

Birch distribution was analyzed at a 10-m scale. Each transect was fragmented into 10-m segments and the number of birch saplings and birch recruits within each 10×10 m segment was summed. As the detectability of small recruiting birch is likely to vary with vegetation and grazing treatment, detection functions were calculated using the software Distance 6.0 (Thomas et al. 2009); details are given in the Appendix. The area under each detection function curve is the detection probability over the transect width and was used as an offset in generalized linear model analyses of birch distribution. Where the number of birch in a treatment–vegetation combination was too low to compute the detection function, the detection probability estimated for that treatment (i.e., across vegetation types) was used. Detection probability of sapling birch was assumed to be 1.0, due to their greater size and visibility.

Birch distribution within 10×10 m transect segments was modeled using logistic regression on presence–absence transformed data (with the 10×10 m transect segments as the observation unit). Treatment (sheep density), habitat productivity, altitude, and block were tested as predictor variables. Block was used as a proxy of the current position of the treeline in the eastern part of the experimental site. Each independent variable was

selected for inclusion in the minimum adequate model using nonsequential backward selection based on likelihood ratio tests (chi-squared) and minimum AIC. Interactions between the retained variables were then investigated in the same manner where appropriate. Separate models were run for birch saplings and birch recruits in R 2.10.0 (R Development Core Team 2009). Logistic regression models were assessed using goodness-of-fit tests (le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares test) and the *c* index (area under the receiver operator curve, ROC) within the Design package in R (Harrell 2009). Model residuals were checked for spatial autocorrelation by plotting correlograms (nfc package in R; Bjornstad 2009). There was deemed to be no spatial autocorrelation where the correlogram *x*-intercept was less than the transect segment length (10 m).

RESULTS

In total, 1165 immature birch (<2 m tall) were located within 291 of the 10×10 m transect segments. Of these, 972 individuals from 186 segments were classified as recruiting within the duration of the grazing experiment (i.e., were estimated to be less than 9 years old, based on basal stem diameter; see *Methods*). In addition, 308 mature birch (>2 m tall) were found; they show the current location of the treeline (Fig. 1).

Birch recruits were more prevalent in the ungrazed enclosures than in either of the grazed enclosures (Fig. 1). Although birch recruits were prevalent in all ungrazed enclosures, at both high and low sheep densities, recruits were less frequent in the west than the east of the experiment (Fig. 1). Altitude, grazing treatment, and block were significant predictors of birch recruit distribution, as were the interactive terms between grazing and altitude and between block and altitude (Table 1). The proportion of transect segments predicted to be occupied by birch recruits decreased with altitude in all treatments (Fig. 2, Table 1). The prevalence of birch recruits did not significantly differ between treatments at the lower altitudes of the experiment, but there was a significant and strong interaction between altitude and treatment in explaining the distribution of birch recruits (Table 1). The predicted proportion of occupied segments was higher in the ungrazed treatment than in either of the grazed treatments at altitudes greater than 1120 m, and the decrease in the proportion of occupied segments with altitude was less steep in the ungrazed treatment than in the grazed treatments (Fig. 2). The altitudinal decrease was steeper in the high-density sheep treatment than in the low-density sheep treatment, although marginally so ($P = 0.052$; Fig. 2, Table 1), with no recruits found at elevations over 1200 m in the high-density sheep treatment. Habitat productivity was not a significant

predictor of birch recruit distribution, and was removed by model selection.

There was a tendency for saplings (immature birch estimated to have been present prior to the experiment initiation) to be more prevalent in the eastern part of the experiment, but no clear difference between treatments (Fig. 1, Table 1). There was thus no evidence that grazing treatment affected the distribution of preestablished birch saplings. The maximum elevation at which birch saplings were found was 1253 m. Residuals from the selected model for both birch recruits and birch saplings demonstrated no spatial autocorrelation at the scale of the transect segments, as determined from the spatial correlogram (x -intercept = 7.04 m for the recruit model and 0.72 m for the sapling model). The area under the ROC (receiver operating characteristic) curve (c index) was greater than 0.8 for both models, indicating that both models performed substantially better than random, although the goodness-of-fit test suggested that the model of recruit distribution provided a better fit to the data than the model of sapling distribution (Table 1).

DISCUSSION

This study provides the first landscape-scale experimental evidence that grazing by large herbivores can limit the altitude of treelines. Surprisingly, even low densities of herbivores had a notable impact on dynamics at the treeline. Birch recruitment at elevations above the treeline was clearly enhanced in enclosures without sheep compared to enclosures grazed by either low or high densities of sheep. This provides strong evidence that herbivory can suppress the altitude of treelines at the landscape scale, and that even low densities of herbivores can markedly limit the speed of treeline advance. In contrast to birch recruiting within the duration of the study, the distribution of preestablished saplings was not affected by grazing treatment. The difference in response of recruits and saplings to the grazing treatments suggests that herbivore suppression of the treeline primarily occurs through the prevention of new recruit establishment, rather than by decreasing the survival of preexisting individuals.

Herbivory and climatic limitations of treelines

Climate and temperature are at the forefront of research on the limitation of treelines (e.g., Korner and Paulsen 2004, Harsch et al. 2009, Kullman and Oberg 2009). However, it has been recognized that herbivores can cause shifts in ecosystem and vegetation state within a range of biomes (Van de Koppel et al. 1997, Van der Wal 2006), and may play a role in regulating treeline position (Cairns and Moen 2004). In this study we have experimentally shown that herbivores, even at low densities, can suppress the treeline. This may partly explain why many treelines are not advancing in

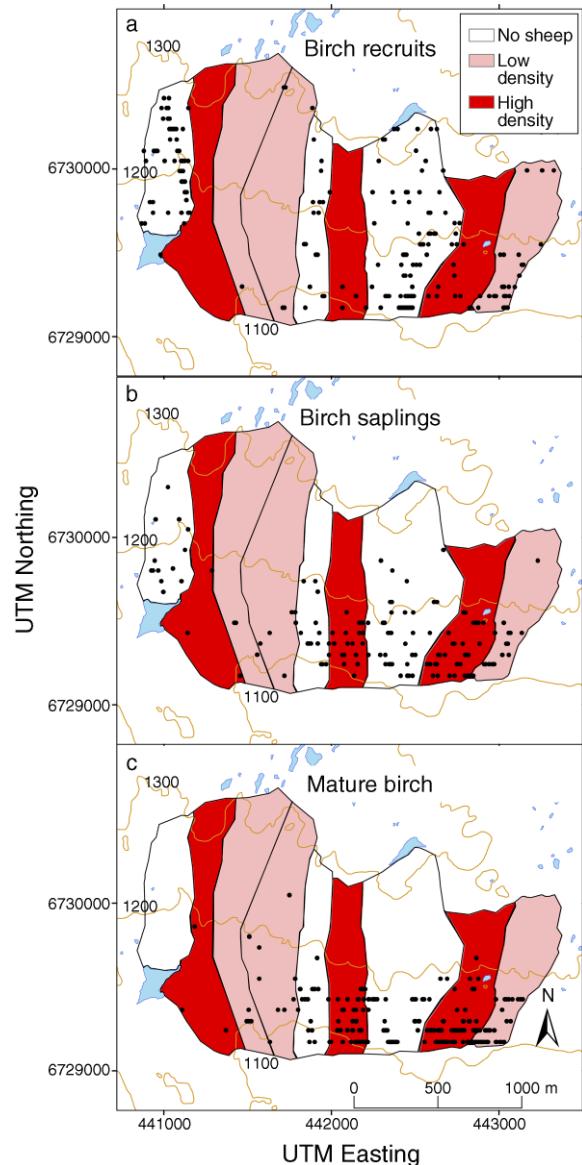


FIG. 1. (a) The distribution of birch recruits (stem diameter ≤ 15 mm), (b) the distribution of birch saplings (stem diameter > 15 mm), and (c) the distribution of mature birch (height > 2 m) across the experimental grazing enclosures. Solid circles indicate the location of individual birches. Experimental treatments were ungrazed (no sheep), low density of sheep ($25/\text{km}^2$), and high density of sheep ($80/\text{km}^2$) and were replicated three times; 100-m contour lines are included to show elevation. Coordinates are from the Universal Transverse Mercator (UTM) grid zone 32V, southern Scandes, Norway.

response to climatic warming on a global scale (Harsch et al. 2009), and in particular may explain differential treeline dynamics within regions (e.g., Dalen and Hofgaard 2005). Climate-driven shrub encroachment onto tundra ecosystems has been shown to be reduced or inhibited by herbivores in small-scale experiments (Post

TABLE 1. Parameter estimates from selected logistic regression models predicting the distribution of saplings and recruits of mountain birch (*Betula pubescens tortuosa*) in the southern Scandes Mountains, Norway.

Parameter	Birch recruits				Birch saplings			
	Coefficient	SE	Wald Z	P	Coefficient	SE	Wald Z	P
Intercept (altitude = 1080 m)	-0.61	0.257	-2.37	0.018	-0.65	0.318	-2.03	0.04
Altitude (m above 1080 m)	-0.01	0.002	-6.02	< 0.001	-0.02	0.003	-6.37	< 0.001
Treatment (low sheep density vs. ungrazed)	-0.14	0.416	-0.34	0.73	-0.29	0.468	-0.63	0.53
Treatment (high sheep density vs. ungrazed)	0.34	0.654	0.52	0.61	0.78	0.419	1.87	0.06
Block (west vs. east)	-2.52	0.454	-5.55	< 0.001	-2.61	0.575	-4.54	< 0.001
Block (central vs. east)	-2.52	0.435	-5.78	< 0.001	-1.46	0.383	-3.81	< 0.001
Altitude × treatment (low sheep density vs. ungrazed)	-0.01	0.004	-3.24	0.001	-0.01	0.005	-1.28	0.2
Altitude × treatment (high sheep density vs. ungrazed)	-0.03	0.009	-3.31	< 0.001	-0.01	0.005	-1.92	0.06
Altitude × block (west vs. east)	0.02	0.003	5.54	< 0.001	0.01	0.006	2.33	0.02
Altitude × block (central vs. east)	0.01	0.004	3.4	< 0.001	0.01	0.005	1.48	0.14

Notes: Model assessment statistics are provided with the *c* index which is the area under the ROC (receiver operating characteristic) curve and the global Wald goodness-of-fit test statistic (GZ) and associated *P*. For birch recruits, *c* = 0.804, GZ = 1.60, *P* = 0.11; for birch saplings, *c* = 0.821, GZ = 4.29, *P* < 0.001. Significant contrasts at the *P* < 0.05 level are shown in bold. Altitude is shown as meters above the minimum recorded of 1080 m.

and Pedersen 2008, Olofsson et al. 2009). However, both of these studies found that the effect of herbivore exclusion was greater than the effect of experimental warming (Post and Pedersen 2008) or ambient temperatures (Olofsson et al. 2009). In our study, herbivory is directly shown to inhibit altitudinal advancement of treelines at the landscape scale over an eight-year period. We suggest that decreases in herbivore density may currently be drivers of the encroachment of shrubs and trees within many arctic and alpine ecosystems. However, the selectivity of herbivores for treeline tree species will vary with herbivores species, with tree species, and with habitat type. For example, reindeer herbivory in lichen heaths promotes birch establishment (Tømmervik et al. 2009). Thus, further research with different herbivore and tree species and at higher spatial and temporal scales is required to find general patterns in the response of treelines to changing herbivore densities. Although climate has been the focus of research into the encroachment of shrubs and trees within arctic and alpine regions, it has been noted previously that anthropogenic changes in land use and cover represent a more important aspect of global change in terms of consequences for ecosystems (Vitousek 1994). Land use change perhaps deserves a greater focus than at present within research into encroachment.

Seeds can disperse far above the treeline (Molau and Larsson 2000); thus, establishment and mortality may be more limiting factors than seed availability at the treeline. However, available sites for seed germination can be increased by grazing (Eskelinen and Virtanen 2005). In the current study, recruits were found over the whole altitudinal range of the experiment, but the prevalence was far lower in the presence of livestock, suggesting that herbivores have a greater impact on recruit mortality than microsite availability. Birch can

regenerate in upland woodlands in the presence of livestock (Pollock et al. 2005), but herbivore-driven reductions in recruitment were found in the current study, particularly at higher altitudes. Climatically driven treeline advance is thus likely to be much slower in grazed areas and may even be completely prevented.

Herbivore density and shifts in the treeline ecotone

Shifts between vegetation states have been linked to grazing pressure and the density of herbivores (Côté et al. 2004, Van der Wal 2006). Although high densities of sheep did have a larger negative effect on birch recruitment within the study presented here, it is notable that even low densities of sheep were adequate to suppress the treeline. This is consistent with the type II model proposed by Cairns and Moen (2004) of decreasing altitudinal treeline migration with increasing herbivore pressure. In this scenario, immature trees are expected to be a preferred forage species over the field vegetation. Herbivore preference for vegetation varies between habitat productivities at the site (Mobæk et al. 2009). However, contrary to predictions, the effect of sheep density on recruit distribution did not vary between habitats of differing productivity. This may be due to foraging herbivores being selective on a hierarchy of spatial scales (Senft et al. 1987). Thus the likelihood of an individual being browsed or grazed depends on both the palatability of the species in question and the palatability of its neighbors (Palmer et al. 2003). Although sheep grazing within the experiment are known to be selective for the more productive habitat, the strength of selection does decrease with increasing density of sheep (Mobæk et al. 2009). Overall, it seems that herbivore density and selectivity outweigh habitat productivity in terms of importance in determining treeline dynamics.

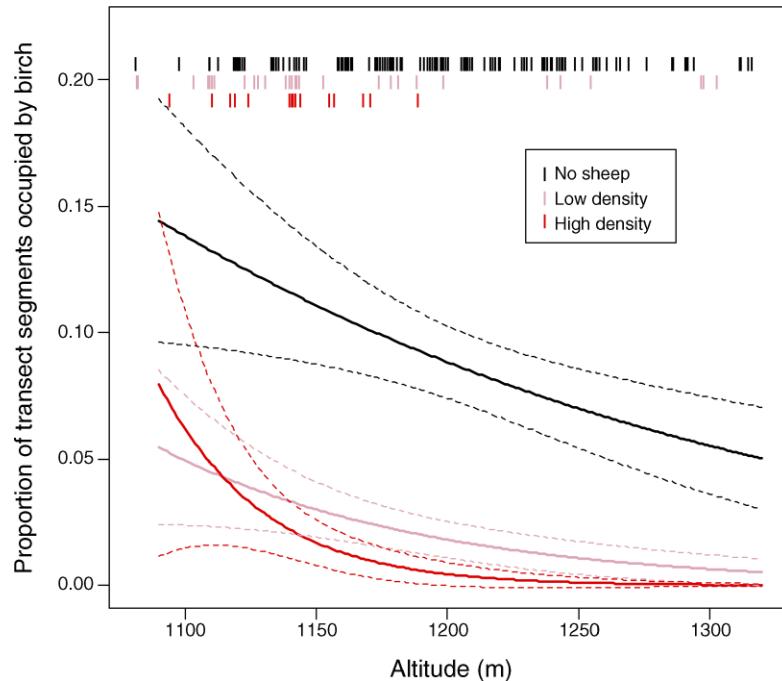


FIG. 2. The proportion of transect segments occupied by birch recruits as a function of altitude across the grazing treatments, as predicted by the selected logistic GLM (generalized linear model) and averaged across covariates and interactions. Means are shown by solid lines; 95% confidence intervals are shown by dashed lines. Short vertical bars at the top show the altitude at which birch recruits were found within each treatment.

Forested vegetation states developing under reduced herbivore density may become particularly resistant to herbivory as trees grow beyond the reach of herbivores. This is demonstrated by the persistence of shrub and tree stands establishing in periods when herbivore density was reduced by disease in both English parklands (Dobson and Crawley 1994) and African savannahs (Prins and Van der Jeugd 1993), for example. The woodland states that result from increased recruitment during these population crashes will persist until mortality of the trees occurs for other reasons. Data presented in the current study suggest that herbivore limitation of the treeline is indeed through recruitment rather than mortality of established individuals. In view of the current decline in free-ranging livestock in many parts of the world (Hester and Brooker 2007, Tasser et al. 2007, Dallimer et al. 2009), we propose that the most dramatic change in response to decreasing densities of livestock in alpine ecosystems is likely to be the state transition from open landscape to forest, with substantial impacts upon species pools, land use, and ecosystem functioning.

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APPENDIX

Estimating the probability of detection of birch seedlings within the treeline ecotone (*Ecological Archives* E091-242-A1).