Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming?

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Abstract. Vegetation at ecotone transitions between open and forested areas is often heavily affected by two key processes: climate change and management of large herbivore densities. These both drive woody plant state shifts, determining the location and the nature of the limit between open and tree or shrub-dominated landscapes. In order to adapt management to prevailing and future climate, we need to understand how browsing and climatic factors together affect the growth of plants at biome borders. To disentangle herbivory and climate effects, we combined long-term tree growth monitoring and dendroecology to investigate woody plant growth under different temperatures and red deer (*Cervus elaphus*) herbivory pressures at forest–moorland ecotones in the Scottish highlands. Reforestation and deer densities are core and conflicting management concerns in the area, and there is an urgent need for additional knowledge. We found that deer herbivory and climate had significant and interactive effects on tree growth: in the presence of red deer, pine (*Pinus sylvestris*) growth responded more strongly to annual temperature than in the absence of deer, possibly reflecting differing plant–plant competition and facilitation conditions. As expected, pine growth was negatively related to deer density and positively to temperature. However, at the tree population level, warming decreased growth when more than 60% of shoots were browsed. Heather (*Calluna vulgaris*) growth was negatively related to temperature and the direction of the response to deer switched from negative to positive when mean annual temperatures fell below 6.0°C. In addition, our models allow estimates to be made of how woody plant growth responds under specific combinations of temperature and herbivory, and show how deer management can be adapted to predicted climatic changes in order to more effectively achieve reforestation goals. Our results support the hypothesis that temperature and herbivory have interactive effects on woody plant growth, and thus accounting for just one of these two factors is insufficient for understanding plant growth mechanics at biome transitions. Furthermore, we show that climate-driven woody plant growth increases can be negated by herbivory.

Key words: adaptive management; browsing; climate change; deer; ecotone; heather; herbivory; pine; reforestation; Scotland; shrubs.

INTRODUCTION

Climate is known to determine the fundamental distribution of biomes, and we have already started to witness ecotone shifts with global warming (Sturm et al. 2001, Harsch et al. 2009, Evans and Brown 2017, Myers-Smith and Hik 2018). However, herbivory has the potential to dramatically change the realized distribution of biomes, and top-down trophic pathways have been shown to affect, for example, the distribution of open tundra ecosystems (Christie et al. 2015, Bråthen et al. 2017) and

savanna (Van Langevelde et al. 2003, Staver et al. 2009, Staver and Bond 2014, Oliveras and Malhi 2016). Large herbivores are important drivers of vegetation state shifts, particularly at tree lines and other areas involving transitions between woody plant dominated states and states with low woody plant cover (Speed et al. 2011, Ripple et al. 2015, Treml et al. 2016, Cromsigt et al. 2018, Olofsson and Post 2018).

By affecting both climate and herbivore populations, human activity has created circumstances where the causes of ecotone changes are hard to disentangle (Oliveras and Malhi 2016, Stevens et al. 2016, Treml et al. 2016, Vuorinen et al. 2017). A growing body of evidence shows the importance of both climatic and top-down trophic factors in driving biome changes, but potential interactive effects between these are still poorly

understood (see, however, Speed et al. 2011, Tremblay and Boudreau 2011, Bråthen et al. 2017, Løkken et al. 2019). In order to adapt herbivory management to prevailing and future climatic conditions, understanding potential interactions between climate and herbivory is crucial.

An example of an ecosystem state shift driven by the combination of climate and herbivores can be found in the Scottish Highlands, UK, where humans have caused one of the most dramatic biome shifts by changing many previously naturally forested areas to open moorlands by felling, fire, and grazing since the Neolithic period (Mather 2004). Concurrent climatic changes toward cooler and wetter conditions around 4000 BP also acted to reduce suitability for some tree species. Even though a reforestation trend has been apparent since the beginning of the 20th century (Mather 2004), strong increases in deer numbers since the 1960s are hampering the return of trees (Scottish Natural Heritage 2016, Rao 2017). To assist reforestation, managers in different parts of the UK have reduced deer densities (Gong et al. 1991, Scott et al. 2000, Rao 2017). Exclusion of deer is a commonly used method, but as fences can have negative effects on the landscape and other species (e.g., grouse), deer culling is also applied. Both of these strategies have resulted in successful forest regeneration (Putman 2003, Rao 2017), but it is unknown whether a warming climate has also contributed to observed tree growth changes (0.4–0.8°C increase 1901–2012; Hartmann et al. 2013) or how it will affect tree growth in the future if mean temperatures keep rising as expected (2.0–3.5°C by the 2080s across UK; Hulme 2002). Earlier studies have estimated that for successful tree regeneration, deer densities need to be at or below 3–5 red deer/km^2 (Rao 2017), but these estimates do not account for variations or change in climate.

In many ecotone areas, herbivory may act as a buffer against climate change by preventing woody plant growth increase (Speed et al. 2012, Christie et al. 2015, Bråthen et al. 2017, Vuorinen et al. 2017, Cromsigt et al. 2018). However, in the management perspective of the Scottish Highlands, this is considered as a negative effect as high deer densities make much more difficult the achievement of the target annual woodland expansion from the Climate Change Scotland Act 2009 (Cairngorms National Park Authority 2016). High deer densities also contribute to maintaining the current, heavily human-altered state of existing native woodlands (Patterson et al. 2014). Nevertheless, from a management perspective, deer are also an important game species and a natural part of highland ecosystems. Wild deer provide a source of local meat and support rural tourism and local economy through recreational visits, sport hunting, and sales of venison (Scottish Natural Heritage 2016). It has been estimated that the annual monetary benefit to the private and public sectors associated with deer is £17.6 million (Scottish Natural Heritage 2016). Thus, balancing between different management targets in a warming climate is crucial.

By assessing radial growth and height growth of key woody species under different temperatures and deer pressures, we addressed the following question: Are tree and shrub radial and height growth driven by (1) herbivore presence, density, and browsing pressure; (2) temperature; or (3) additive or interactive effects of herbivores and temperature? In addition, to inform management of deer and reforestation under future climate change and conservation requirements, we aim to estimate the increases in deer density and browsing pressure that would prevent the predicted tree growth increases under climatic warming.

METHODS

Study area

The study area, located in the Mar Lodge Estate, Cairngorms National Park, Scotland, UK (57°00′ N 3°32′ W, 300–520 m above sea level), is dominated by remnant Caledonian pine forest and open moorlands. The main browser is the red deer *Cervus elaphus*, with low number of roe deer *Capreolus capreolus* and mountain hare *Lepus timidus* also occurring in the region (Rao 2017). There are no sheep or other ungulate herbivores in the study area. The study area contained 15 deer exclosures, ranging in size between 0.016 and 480 ha, with fences that were erected at different times between 1959–1999 and taken down 2012–2013 (with some exceptions, see Appendix S1: Fig. S1, Table S1). After 1995, the land owner, the National Trust for Scotland, embarked on larger-scale restoration of pine forests through reduction in numbers of deer in the whole study area of 12,487 ha through culling. This has resulted in a reduction of deer densities from approximately 15 deer/km^2 to near zero in 15 yr (Fig. 1a; for more information on deer count methods see Rao [2017]). Both red and roe deer were managed under the deer reduction program, but only red deer numbers were monitored. In addition to yearly counts of individuals, deer have been monitored by counting red deer and roe deer pellets (not separated by species) in 17 10 × 10 m quadrats since 2002 (Appendix S1: Fig. S1; for methods, see Rao [2017]).

The nearest weather station, located approximately 6 km east from the study area (Braemar, 57°01′ N 03°40′ W, 327 m above sea level), gave a source of daily temperature data covering the whole deer monitoring period (information provided by the National Meteorological Library and Archive—Met Office, UK; © Crown Copyright 2017). The data shows variation between 5.3°C and 7.7°C in yearly mean temperatures, with an annual average of 7.0°C, but no consistent warming trend across the study period (Fig. 1a).
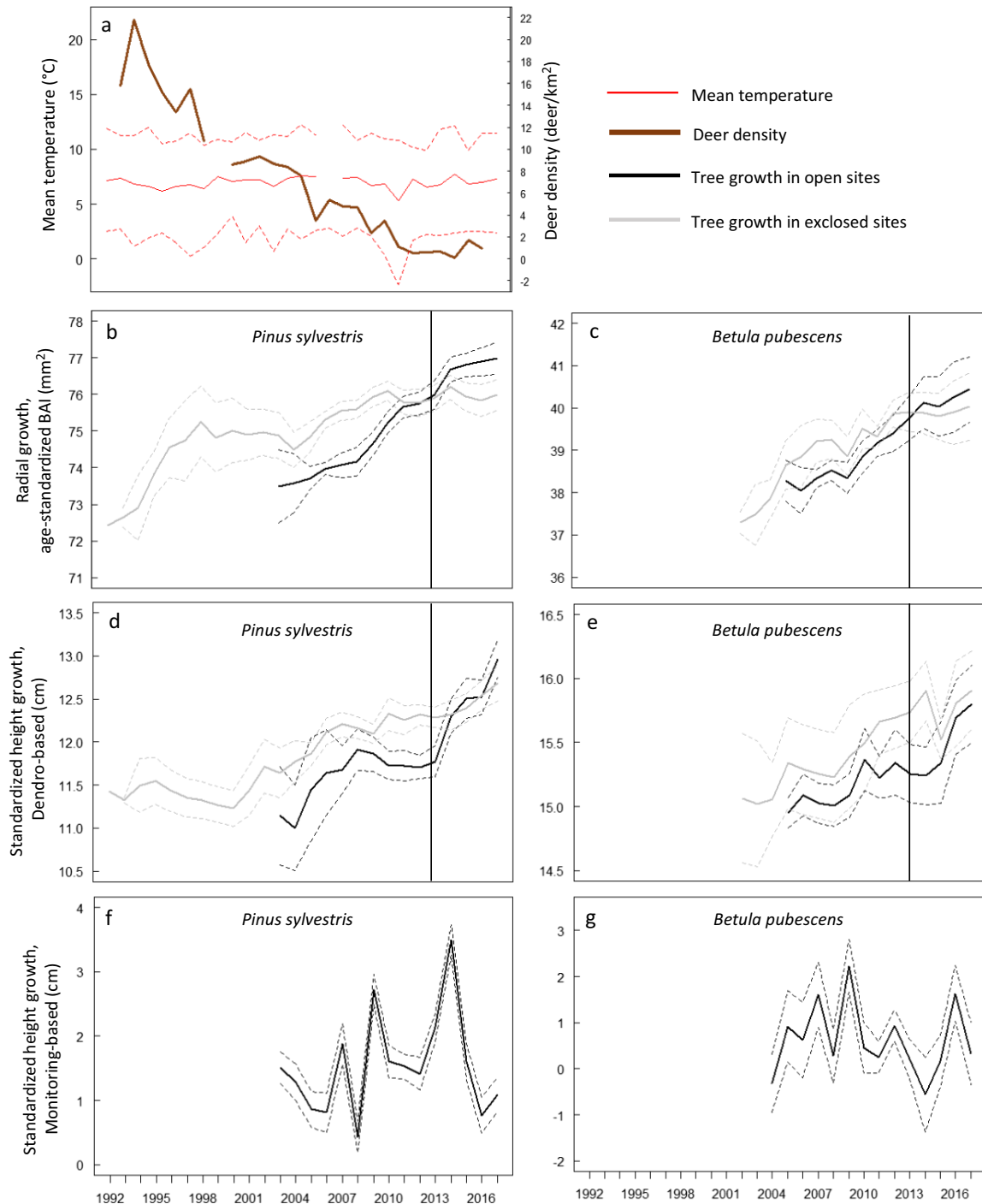
FIG. 1. Temperature, deer density, and tree growth trends 1992–2017. (a) Mean annual temperatures, summer (June–August), and winter (December–February) temperatures (upper and lower dashed red lines, respectively) recorded at Braemar weather station (Information provided by the National Meteorological Library and Archive—Met Office, UK; © Crown Copyright 2017), and red deer densities (Rao 2017). (b–e) Radial growth (BAI, basal area increment) and height growth of pine and birch, based on dendroecological measurements (mean ± SE [dashed lines]). (f, g) Height growth of pine and birch, based on monitoring measurements (mean ± SE [dashed lines]). Data points of years with less than three individuals have been excluded. Note that, even though most of the fences were taken down 2012–2014 (vertical lines), they are depicted here as exclosures. In 1997, the deer survey was not undertaken and, in 2005, temperature information lacked from some summer months, resulting in missing data from these years. The oldest individuals from open plots shown in the graph were not established before 2002, and thus there is no growth data available before that year. For an equivalent graph on heather growth, see Appendix S1: Fig. S2.

Dendroecological methods

A dendroecological approach was used to study the effects of deer presence and red deer density. We sampled paired individuals of three species playing central roles for reforestation, vegetation structure, and composition: Scots pine (*Pinus sylvestris*), downy birch (*Betula pubescens*), and heather (*Calluna vulgaris*). We sampled one individual inside of an exclosure and one outside, at each sampling spot in October–November 2017. As we were only permitted to destructively sample a small number of individuals, we standardized our sampling by first subjectively defining paired areas that matched in their growing conditions inside and outside the fence to minimize the variation caused by environmental variables not relevant for our study question. When selecting these areas, slope, aspect, field layer vegetation, moisture conditions, amount of rocks and tree shading were considered (Appendix S1: Fig. S2). However, as precisely similar sites were not always found outside and inside the exclosure, we also measured slope, aspect, and tree shading at each sampling location. Tree shading was estimated by establishing a 10 m radius circle around each individual, measuring the height and the distance to the sampled individual of all tree individuals growing inside the circle, and by summing the height : distance ratio of these tree individuals (Appendix S1: Fig. S3).

Within the paired areas, we selected a random primary starting spot and sampled the nearest individual of each target species, excluding individuals >220 cm in height and as such out of red deer browse-reach, and individuals located ≤5 or ≥25 m from the fence line, to standardize potential edge effects. Due to tree-regeneration management restrictions, we were permitted to sample only one pair of each species at each small fenced area (<10 ha) and two pairs at each large fenced area (>10 ha). Species absence in some areas constrained sampling further (Appendix S1: Table S1), resulting in a sample size of 13 pairs for pine, 6 for birch, and 18 for heather, with no significant height or diameter differences between exclosure and open plot individuals.

Sampled trees were cut at ground level. Shrubs stems were cut at 10–15 cm (length) below the base, but no root collar was reached. One disc at the base of each stem was cut and stored at room temperature in a well-ventilated space. Discs were prepared for reading of growth rings by taking thin sections of 20–30 μm with a GSL1 microtome (Fritz Hans Schweingruber, Birmensdorf, Switzerland) (Gärtner and Schweingruber 2013). Sections were stained by using a solution of aqueous Astra Blue 1 g/1,000 mL and aqueous Safranin O Dye 1 g/1,000 mL (1:1) (Gärtner and Schweingruber 2013) and a staining time of 3 minutes, which turns lignified structures pink and the cellulose of unlignified cells blue (Vazquez-Cooz and Meyer 2002). After dehydration with ethanol (Gärtner and Schweingruber 2013), sections were fixed permanently on microscope slides with Canada Balsam, applied on the sections and dried in an oven at 60°C for at least 12 h (Gärtner and Schweingruber 2013, Tardif and Conciatori 2015). Growth ring widths were measured manually with the Leica Application Suite program (LAS version 4.5.0, Core), using a Leica M165 C microscope system with MV170 HD camera (Leica Microsystems, Wetzlar, Germany). For each disc, four radii separated by 90° were measured when possible to account for irregularities in growth (Myers-Smith et al. 2015), with the exception of symmetrical large pines and birches, for which only two radii separated by 180° were measured (in these cases, a 1 cm wide piece was cut along diameter of the disc for micro-sectioning). Measurements of radii were averaged for each growth ring and converted to basal area increment (BAI; wedging rings were accounted for as zeros when absent at a certain radius), assuming that ring circumference can be approximated by a circle (Biondi and Qeadan 2008), using the dplR-package (Bunn 2008). To account for the growth increase induced by increasing age, data for each species were standardized using a linear model with log-transformation for BAI values, $\log_e(\mathrm{BAI}) = a + b \times \mathrm{Age}$. The back-transformed residuals from these models were then used as response variable in the analysis (Speed et al. 2011). These values allow us to model the average growth responses of the population comprising of trees with different heights.

Radial growth might not be a good indicator of height growth, as herbivores might keep shrubs and trees low in a "browsing trap" (Staver and Bond 2014, Olofsson and Post 2018), even if radial growth is not constrained. Thus, studying only ring widths may produce results not relevant for management that is concentrated on reforestation and establishing trees that grow tall enough to escape browsing. To overcome this constraint, we estimated annual height growth for sampled trees by taking four additional discs at regular intervals along the main stem (Myers-Smith et al. 2015), counting the number of rings and calculating annual height growth based on disc cut heights. When discs were too far from each other to capture annual growth, linear growth was assumed across years. Height growth values were standardized in the same way as ring growth values.

Population-level tree monitoring

As the dendroecological approach incorporates both direct (browsing) and indirect (e.g., plant–plant competition) effects of deer, we also took advantage of the long-term tree height and browsing monitoring conducted in the study area to be able to analyze direct browsing effects. This monitoring was done at the same quadrats that were used for deer pellet monitoring (Appendix S1: Fig. S1). In 2002, 17 10 × 10 m quadrats were established and 20 tree individuals marked for monitoring in each quadrat (unless the number of individuals was lower than 20, in which cases all individuals were marked). In 2007 and 2012, new tree cohorts were added, varying from 4 to 20 individuals per each quadrat. Each year 2002–2017 in July–August, the height of

all marked trees was measured and the number of browsed twigs counted. This resulted in height observations of 870 pine individuals and 78 birch individuals, but due to gaps in browsing and temperature data, some of the observations were left out of the analyses. Height observations were converted to yearly height growth values and standardized as described above for trees sampled for the dendroecological analyses, but using tree height rather than age.

It is important to note that the tree monitoring approach is not directly comparable with the dendroecological approach, since the study locations differed (Appendix S1: Fig. S1). Furthermore, these two approaches differ in the part of the tree population they address, giving complementary information: the dendroecological approach only includes individuals that have survived to the sampling date, and thus addresses the growth potential of surviving trees at the individual level; the monitoring approach takes into account individuals that have shown negative growth (i.e., severe browsing of the leading shoot) or have even been killed by browsing, thus addressing the average growth at tree population level.

Statistical analyses

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We modeled annual age-standardized BAI, and age- and height-standardized tree height growth as a function of mean temperature at Braemar weather station for corresponding years, different types of deer factors, their interaction, and measured environmental covariates (slope, aspect, shading caused by trees) by using the lme function of the nlme package (Bates 2007), separately for each species. See justification for using mean temperature as a climate variable in Appendix S1: Fig. S4. In the first model versions, we also included "exclusion time" (years since fence was erected) as a covariate, but as it was never significant, we ran the final models without it.

Three versions of the above-described models were constructed to assess three types of deer effects (i.e., deer presence, red deer density, and browsing) separately. (1) To study whether deer presence (related to fencing program) alters growth response to temperature, the deer exclosure treatment (open vs. exclosed site) was used as a binary explanatory variable. (2) To study the effects of herbivore density (related to culling program), red deer density data was used as a continuous explanatory variable. As an additional analysis, we also used deer pellet counts from the nearest pellet monitoring site, as they are often used to indicate the density of herbivores but may give a different result than direct deer density measurements due to spatial heterogeneity in habitat use. If the nearest pellet monitoring site was located on the other site of the river that flows thought the study area, data from the nearest site on the same site of the river was used. For these models, only plants sampled outside the exclosures were included to make the study design more balanced (i.e., not biased toward zero deer values). (3) To study the local effects of browsing intensity, the proportion of browsed twigs was used as a continuous explanatory variable.

Random intercepts were fitted to account for the nesting of individuals within sites for each model. After this, there was no spatial autocorrelation detected in the model residuals (Appendix S1: Table S2). After applying model selection, we found that multiple models had a similar degree of support based on AIC values, and thus applied model averaging to avoid model selection uncertainty (Johnson and Omland 2004, Cade 2015, Dormann et al. 2018). For model averaging, we used the MuMIn package (Barton 2016): all possible models between null model and a full model with all explanatory variables and the interaction of climate and herbivory factors were built using the dredge function, and coefficient estimates were averaged across these models (weighted by AIC) by using the model.avg function. See goodness of fit of the models in Appendix S1: Table S3.

To provide a tool to estimate the increase in deer pressure that would counter the predicted tree growth increase through expected climatic warming, we visualized predictions from all models that included a continuous deer factor by using heat-maps of tree growth across temperature and deer factor axes. Note that full deer factor and temperature factor data ranges are used for predictions even when all deer and temperature combinations were not present in our data set. Thus, the further away a coordinate is from the observation points, the less reliable the prediction is.

RESULTS

Trends in time

Dendroecological measurements resulted in growth series for the period 1992–2017 for pine, 2002–2017 for birch, and 1994–2017 for heather. Tree growth (both pine and birch) increased in the exclosures since the years in which the fences were erected, and increased outside the exclosures at later dates in line with the deer culling program (Fig. 1a–e). However, the tree height monitoring data did not show consistent increasing trend (Fig. 1f, g). We also found no consistent trends in heather growth over time (Appendix S1: Fig. S5).

Effect of deer presence on temperature response

Pine growth was more sensitive to temperature changes in the presence of deer than the absence of deer, as shown by significant interaction terms (for radial growth, $z = 2.1$, $P = 0.038$; for height growth, $z = 3.4$, $P < 0.001$; for full model output, see Appendix S1: Table S4). Outside the exclosures, pine growth responded positively to increasing temperatures: with a 1°C temperature increase, radial growth increased by
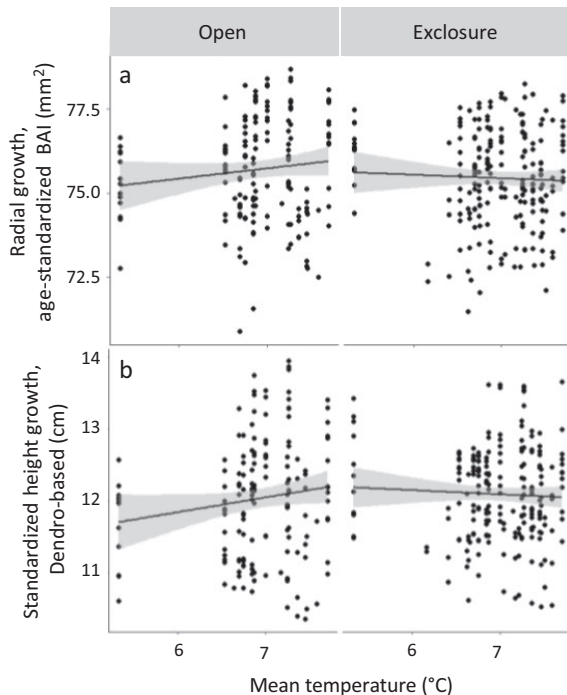
FIG. 2. Pine radial and height growth along a gradient of mean annual temperature in each deer herbivory treatment. Black points depict raw data and black lines linear growth–temperature relationship with SEs (gray), based on a model with deer as a presence-absence explanatory variable.

0.26 ± 0.16 mm^2 (mean $\pm$ SE; Fig. 2a) and height growth by 0.27 ± 0.07 cm (Fig. 2b). Inside the exclosures, there was no trend to be seen (for radial growth, slope -0.01 ± 0.05, and for height growth -0.02 ± 0.06). Differences in slopes between treatments were small, however. We observed no significant interactive effects of deer presence and temperature on birch or heather growth (Appendix S1: Table S4).

Deer density effects and temperature effects

For pine, both deer density and mean temperature affected radial and height growth, but there was no evidence of interactive effects (Table 1). Model-based predictions showed that pine growth responded positively to mean temperature, but that red deer have the potential to suppress the growth increase (Fig. 3a, b). Model predictions indicate that 1°C of warming equates to an increase of 0.4 mm^2 in annual radial growth. From our findings, this was negated by an increase of 1 deer/km^2 density (Fig. 3a). The same degree of warming was found to equate to an increase of 0.2 cm in annual height growth, which could be negated by an increase of 3 deer/km^2 density (Fig. 3b). The effects of pellet density and mean temperature on pine height growth showed the same type of patterns but, for radial growth, we found a pellet × temperature interaction where

responses weakened when temperature increased and pellet number decreased (Appendix S1: Fig. S6, Table S5). For birch, no significant effects were found.

For heather, we found a significant interaction effect of deer density and temperature ($z = 1.54$, $P = 0.043$; Table 1). At low annual temperatures (<6.0°C), radial growth increased with increasing deer density and was negatively related to increasing temperature. At high temperatures (>6.0°C), growth was negatively related to both deer density and temperature (Fig. 4). The deer pellet model showed no significant effects on heather growth (Appendix S1: Table S5).

Deer browsing effects and temperature effects

We found an interactive effect of mean temperature and browsing intensity (percentage of shoots browsed) on pine height growth (Table 2). When <60% of pine shoots were browsed, height growth increased with increasing temperature and decreased with increases in deer browsing damage: 1°C warming equated to an increase of 0.3–1.5 cm annual growth, depending on browsing intensity, which could be negated by increase from 15% to 40% on the browsing intensity scale, depending on mean temperature. When >60% of shoots were browsed, height growth of pines was negatively related to increasing temperature (Fig. 3c). In general, the tree height monitoring data (which included trees that since died, as previously explained) indicated lower annual pine growth rates than the dendroecological approach (which included only trees surviving at time of sample in 2017), with a maximum of 3.6 cm/yr even at moderate browsing pressure (Fig. 3c). We found no significant effects of browsing intensity on birch growth (Table 2).

DISCUSSION

In this study, we have found evidence showing that herbivory and climate interact to determine woody plant growth at a forest–moorland ecotone. The temperature responses of pine and heather varied with herbivory pressure, and this demonstrates how herbivory might counteract or amplify the effects of temperature for these species. Temperature responses of radial and height growth of pine individuals were stronger in the presence of deer, and growth was driven by counteractive forces of temperature and herbivore density. At the tree population level, pine height growth was driven by the interactive effects of browsing and temperature, with temperature response differing below and above a threshold of 60% browsing intensity. Furthermore, we found some support for heather radial growth also being affected by interactions between temperature and herbivory, indicating different growth responses to deer density below and above a threshold of 6.0°C. Our results highlight the vital need to understand interactive and additive impacts to be able to responsively manage large herbivore dynamics in a changing climate.

TABLE 1. Coefficients for the models with the effects of deer density, mean temperature, and covariates on tree and shrub growth by analysis, conducted separately for each growth measurement type.

Parameters	Importance	Estimate	SE	z	P
Pine ($n = 138$)					
Radial growth					
Intercept		73.16	2.03	35.84	<0.001
Mean temperature × Deer density	0.73	−0.15	0.13	1.08	0.28
Mean temperature	0.92	0.39	0.15	2.64	**0.008**
Deer density	1	−0.39	0.05	7.37	**<0.001**
Tree shading	0.29	−0.01	0.02	0.15	0.882
Slope	0.29	−0.01	0.03	0.12	0.902
Aspect	0.74	0.01	0.01	0.65	0.517
Elevation	0.3	0	0.01	0.13	0.898
Height growth					
Intercept		10.41	1	10.34	<0.001
Mean temperature × Deer density	0.79	−0.11	0.06	1.69	0.09
Mean temperature	0.93	0.2	0.07	2.71	**0.007**
Deer density	0.81	−0.06	0.03	2.23	**0.026**
Tree shading	0.72	−0.02	0.01	0.39	0.694
Slope	0.72	−0.04	0.02	0.46	0.646
Aspect	0.72	0.01	0	0.45	0.654
Elevation	0.26	0	0	0.04	0.971
Birch ($n = 74$)					
Radial growth					
Intercept		42.864	5.7	7.5	<0.001
Mean temperature × Deer density	0.07	−0.098	0.08	1.2	0.24
Mean temperature	0.34	0.225	0.25	0.9	0.38
Deer density	0.44	0.042	0.32	0.1	0.9
Tree shading	0.52	0.039	0.02	0.4	0.66
Slope	0.55	−0.107	0.06	0.4	0.69
Aspect	0.56	−0.046	0.03	0.3	0.77
Elevation	0.25	−0.002	0.01	0	0.98
Height growth					
Intercept		15.543	1.43	10.8	<0.001
Mean temperature × Deer density	0.02	−0.005	0.03	0.1	0.88
Mean temperature	0.28	−0.048	0.09	0.5	0.59
Deer density	0.25	−0.003	0.06	0	0.97
Tree shading	0.25	−0.002	0.01	0.1	0.95
Slope	0.25	−0.01	0.03	0.1	0.96
Aspect	0.28	−0.007	0.01	0.1	0.9
Elevation	0.26	0.002	0	0.1	0.94
Heather ($n = 148$)					
Radial growth					
Intercept		3.02	1.61	1.86	0.062
Mean temperature × Deer density	0.89	−0.05	0.03	1.54	**0.043**
Mean temperature	0.56	0	0.13	0	0.5
Deer density	0.78	0.06	0.18	0.35	0.23
Tree shading	0.76	−0.03	0.01	0.5	0.615
Slope	0.27	−0.02	0.04	0.08	0.94
Aspect	0.32	0	0.01	0.13	0.897
Elevation	0.3	0	0.01	0.09	0.93

Notes: Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson 2004 equations), z values are regression coefficients divided by SEs, and $Pr(>|z|)$ values are probabilities of calculated z > tabulated z. Significant P values are shown in boldface type.

Our data demonstrate an overall positive effect of the deer reduction program on pine growth over time at the study area (see also Rao 2017), but show that temperature also plays a role in determining pine growth. We found that pine individuals growing in the presence of deer were more responsive to temperature. This might reflect reduced intraspecific plant–plant competition outside the exclosures (Appendix S1: Fig. S3; Saunders
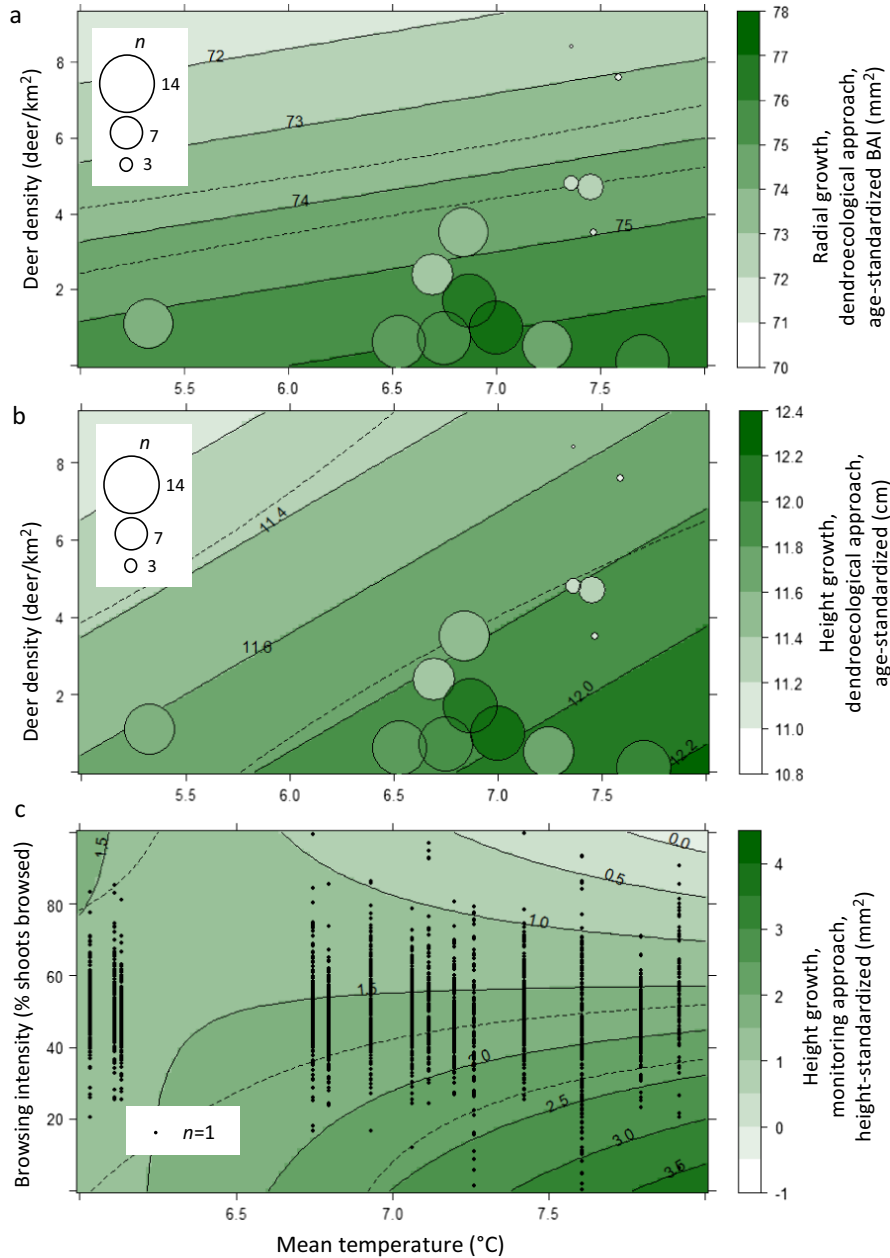
Fig. 3. Predicted pine (a) radial and (b, c) height growth along temperature, deer density (a, b), and browsing intensity (c) gradients as predicted by the respective models (Table 1): y-axis indicates deer pressure, x-axis indicates temperature, and color shows predicted growth. Standard errors are plotted for contour lines (a) 74 mm², (b) 11.6 cm, and (c) 2.0 cm with dashed lines. Observation points are depicted as circles with size representing sample size at each point and color the mean growth in panels a and b, and as black points in panel c. Note that model predictions get less reliable when moving further away from the data points. The difference between model prediction (color on background) and observation points (color in circles) represents the deviation between model prediction and the average observed values on each circle.

and Puettmann 1999, Nishizawa et al. 2016). In the landscape kept open by deer, solitary tree individuals might be able to take advantage of rising temperatures more effectively than individuals in dense stands where higher tree density can constrain growth. Furthermore, increased vulnerability of lone trees to cold temperatures might contribute to observed trends (Speed et al. 2011):

individuals with no shelter provided by neighboring trees and with potentially browsing damage might suffer from cold periods more than unbrowsed individuals in fences where higher tree density potentially moderates temperature changes (Karlsson 2000, Oerlander and Karlsson 2000, Heithecker and Halpern 2006). Thus, herbivory presence per se does not seem to prevent potential
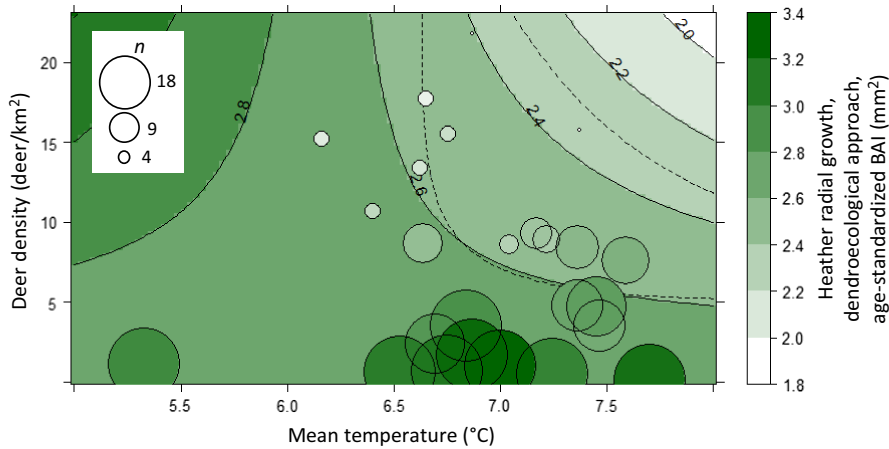
FIG. 4. Heather radial growth along temperature and deer density gradients as predicted by the model with deer density. The *y*-axis indicates deer pressure, *x*-axis indicates temperature, and color shows predicted growth. SE limits are plotted to contour line 2.4 with dashed lines. Observation points are depicted as circles with size representing sample size on each point and color the mean growth. Note that model predictions get less reliable when moving further away from the data points. The difference between model prediction (color on background) and observation points (color in circles) represents the deviation between model prediction and the average observed values on each circle.

TABLE 2. Coefficients for the models with the effects of browsing and mean temperature on tree height growth by analysis.

Parameters	Importance	Estimate	SE	z	P
Pine ($n = 2{,}784$)					
Height growth					
Intercept		−3.12	5.15	0.61	0.545
Mean temperature × Browsing intensity	0.72	−0.02	0.01	1.9	**0.047**
Mean temperature	0.85	0.95	0.69	1.37	0.17
Browsing intensity	1	0.07	0.1	0.72	0.474
Birch ($n = 412$)					
Height growth					
Intercept		−0.264	2.3	0.1	0.91
Mean temperature × Browsing intensity	0.06	0.019	0.02	0.9	0.38
Mean temperature	0.48	0.293	0.42	0.7	0.49
Browsing intensity	0.34	−0.019	0.09	0.2	0.83

Notes: Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson 2004 equations), *z* values are regression coefficients divided by SEs, and Pr($>|z|$) values are probabilities of calculated $z >$ tabulated z. Significant *P* values are shown in boldface type.

growth increases in response to temperature increase, but it might actually strengthen the response of individual trees through indirect effects. However, differences in temperature responses between treatments were small, suggesting a negligible management significance of the interaction. In addition, further modeling makes clear that herbivory has the potential to suppress positive temperature effects on growth when browsing pressure is high enough.

Tree height monitoring showed that at the population level, average pine height growth in the area was at maximum 3.6 cm/yr, and approached zero when browsing has intensified (Fig. 3c). However, from our findings, a 2.0–3.5°C warming as predicted by the 2080s (Hulme 2002) could result in a mean increase of 2.5–4.4 cm/yr in

annual pine growth, an effect size that would, over decades, have power in assisting forest regeneration, but this relationship was found to apply only if the percentage of shoots browsed remained under 60%. Above this threshold, the temperature–growth response was negative. Thus, we have shown that at a tree population level, pine height growth is driven by interactive effects of browsing intensity and temperature. We propose that this may be because heavy browsing exposes trees to stress related to higher temperatures, for example, to plant–plant competition or water stress (Bansal et al. 2013).

For the pine individuals that survived the earliest successional phase (i.e., those sampled for our dendroecological analyses), estimations of growth were higher, varying between 11.2 and 12.2 cm/yr for height growth,

and 72 and 76 mm^2/yr for radial growth. However, they were less affected by temperature. If the climate warms by 2.0–3.5°C as expected by the 2080s, our results suggest that height growth could increase by 0.4–0.7 cm/yr and radial growth by 0.8–1.4 mm^2/yr (although temperatures above 7.7°C would be an extrapolation of our findings). Thus, a warmer climate might have ecologically less significant effect on growth of established tree individuals than on the average growth at tree population level, which also includes tree deaths (see also, e.g., Lutz et al. 2013, Hedwall et al. 2015). Our findings indicate that individual pine radial and height growth are driven by temperature and herbivore density, and that an increase of 6.0–10.5 and 2.0–3.5 red deer/km^2, respectively, could negate the expected increases in height and radial growth of pine along a warming climate gradient.

Combined effects of multiple factors, such as the climate × herbivory interactions revealed here, pose challenges for ecotone management. By using the model predictions illustrated in Fig. 3a, b, it is possible to define plant growth goals and determine the herbivory density that is most likely to allow such a growth rate under specific climatic conditions. For instance, if we assume a warming of 0.5°C (with expected mean annual temperature being 7.5°C), and select an example management aim of achieving mean radial growth of pine of 75–76 mm^2/yr, then deer density could be allowed to vary between 1.3 and 3.2 deer/km^2. However, there are multiple uncertainties associated with these predictions. Extrapolating outside observation points might result in erroneous predictions. Low explanatory power of the browsing intensity analyses and modest effect sizes of deer density analysis suggest that environmental variables not measured in this study, such as potential water and nutrient availability, may operate as barriers to growth increase and be as relevant for management as deer and temperature. Furthermore, as different climate variables measured at the study area were found to be collinear (Appendix S1: Fig. S4), it is also possible that instead of mean temperature, observed effects might be driven by other climatic dimensions, for example the number of frost days or minimum temperatures during growth period, and thus mean temperatures as such might not be reliable for making predictions (see also Franke et al. 2017). Furthermore, we do not know how increased CO_2 levels have contributed to observed patterns along temperature changes, or how they might affect future growth (Kurepin et al. 2018). If increasing temperatures affect plant palatability and thus change browsing pressure (see, e.g., Moreira et al. 2014, Stark et al. 2015, Kivimäenpää et al. 2017), growth predictions become even more challenging.

The management objective of the study area and of many other parts of the Scottish highlands (The National Trust for Scotland 2012, Cairngorms National Park Authority 2016, Scottish Natural Heritage 2016, Cairngorms National Park Authority 2017) is to expand native pine forest, and thus to prioritize tree growth over deer populations until forests have established. Our findings indicate that success could be achieved at different deer densities depending on prevailing temperatures. However, even though areas with trees that have already survived the first phase of forest succession might be able to tolerate browsing better in a warmer climate, even small increases in deer numbers might endanger forest regeneration in a warmer climate if browsing passes the 60% threshold that we detected here. This highlights the importance of low deer numbers for successful population-level growth even under a warmer climate. In the longer term, once woodland has been restored, regeneration should be able to proceed in the presence of a limited deer population (The National Trust for Scotland 2012, Cairngorms National Park Authority 2017).

Adapting deer management solely based on pine growth aims might have impacts on other aspects of the vegetation. We did not find an effect of browsing or temperature on the growth of birch, but our sample size of birch was limited due to its rarity at the sites, and previous studies have shown strong deer browsing effects on birch (compare, e.g., to Tanentzap et al. 2013). Furthermore, management might result in undesired changes to other species groups such as dwarf shrubs. One out of three of our heather growth models identified interactive effects of deer density and temperature, where the direction and magnitude of the deer density effect changed at a specific temperature threshold. Heather growth responded negatively to increasing temperature, which might be caused by negative collinearity of mean temperature and snow cover that protects shrubs from wind, drought stress and herbivory during winter (Ueda et al. 2002, White et al. 2009, Ossi et al. 2015, Gilbert et al. 2017). The reduction in heather growth with increasing deer density when temperatures were above 6.0°C, compared with the increase with deer densities below 6.0°C, might reflect indirect effects of snow cover: when snow reduces access to shrubs, deer more frequently browse trees (Ueda et al. 2002), and thus can reduce tree shading of heather in subsequent growing seasons. Temperature may also change the relative palatability or compensatory growth tendency of heather (Hawkes and Sullivan 2001) in relation to other forage species. Our results imply that in a warmer climate, heather growth may decrease in our study area, and that any increased browsing of heather could amplify this negative warming effect by further reducing its growth.

The Scottish highlands are an example of an environment where human intervention has extirpated large carnivores and supported increases in herbivore densities with a net result of changing the ecosystem from plant–herbivory–predation dynamics to be dominated by plant–herbivory interactions (Estes et al. 2011, Ripple et al. 2014, Svenning et al. 2016). Increases in wild ungulate numbers have occurred across many northern latitude areas, resulting in major vegetation changes (Côté

et al. 2004), and in many environments domestic herbivores are primary drivers of plant system structure (Ross et al. 2016, Speed et al. 2019). In tropical regions, a prime example is African savannas where humans have decimated populations of large natural herbivores in many regions, and replaced them with livestock (Ripple et al. 2015, Hempson et al. 2017). Some ecosystems, such as arctic tundra, may naturally be two trophic-level systems, (vegetation and herbivores), as the low primary productivity precludes the third, predator trophic level (Aunapuu et al. 2007). When plant-herbivory interactions dominate, as they do in the above-mentioned ecosystems, herbivory effectively suppresses plant growth, potentially creating landscapes devoid of trees and tall shrubs. However, global warming changes this balance by increasing primary productivity. This increase in productivity can be manifested in changed vegetation structure (i.e., tree or shrub advance), or it can cascade to the herbivore trophic level, where increased herbivory may negate the warming-induced growth increases and vegetation shifts. In the Scottish Highlands, deer management has a key role in determining which one of these directions might be taken in future. To manage vegetation toward desired directions, the interactive roles of herbivory and climate, as elucidated here, need to be accounted for across the globe.

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SUPPORTING INFORMATION

DATA AVAILABILITY