

Climate change intensification of herbivore impacts on tree recruitment

Jedediah Brodie^{1,*}, Eric Post³, Fred Watson⁴ and Joel Berger^{1,2}

¹Wildlife Biology Program, and ²Wildlife Conservation Society, Northern Rockies Field Office, University of Montana, Missoula, MT 59812, USA

³Department of Biology, Pennsylvania State University, State College, PA 16802, USA

⁴Division of Science and Environmental Policy, California State University, Monterey Bay, Seaside, CA 93955, USA

Altered species interactions are difficult to predict and yet may drive the response of ecological communities to climate change. We show that declining snowpack strengthens the impacts of a generalist herbivore, elk (*Cervus elaphus*), on a common tree species. Thick snowpack substantially reduces elk visitation to sites; aspen (*Populus tremuloides*) shoots in these areas experience lower browsing rates, higher survival and enhanced recruitment. Aspen inside herbivore exclosures have greatly increased recruitment, particularly at sites with thick snowpack. We suggest that long-term decreases in snowpack could help explain a wide-spread decline of aspen through previously unconsidered relationships. More generally, reduced snowpack across the Rocky Mountains, combined with rising elk populations, may remove the conditions needed for recruitment of this ecologically important tree species. These results highlight that herbivore behavioural responses to altered abiotic conditions are critical determinants of plant persistence. Predictions of climate change impacts must not overlook the crucial importance of species interactions.

Keywords: elk; plant demography; snowpack; species interactions; Yellowstone

1. INTRODUCTION

Interactions among organisms define the distinction between fundamental and realized niches and are expected to be of considerable importance in determining species-level responses to climate change [1,2]. A large literature has focused on direct organismal responses to changes in climate [3,4], but it is increasingly clear that changes in ecological communities [2,5] and the persistence of particular species [6] may be at least as strongly determined by altered species interactions as by direct physiological impacts. Predicting species' responses to projected climate change is, by necessity, limited to species distribution models or environmental niche models; these are beginning to incorporate species interactions, although focusing mainly on competition or facilitation [7–9].

Further complicating species-level predictions, trophic interactions can greatly influence plant and animal abundance, and the strength of these interactions can be altered by climate change. Thus, by affecting the strength of a trophic interaction, climate change can indirectly influence abundance. Climate change can influence animal foraging behaviour, thereby affecting how strongly they interact with their resources; these novel behavioural interactions can have implications for ecosystem function [10], though they may be difficult to predict in advance. For example, reduced snowpack levels have either strongly increased [6] or decreased [11] the strength of trophic interactions in different temperate-zone systems.

Our understanding of the relationships and interactions between direct (abiotic changes) and indirect (altered species interactions) impacts of climate change remains limited. Non-experimental studies rely on statistical models to assess the relative influence of these impacts. This can be problematic in, for example, herbivore–plant interactions where plants are affected directly by changing climatic conditions (e.g. [12]) and indirectly by altered herbivore behaviour (e.g. [6]), but where herbivore abundance also responds to climate (e.g. [13]). In such cases, only experiments can reliably tease apart the relative influence of climate, herbivory and their interactions on plant demography. Here, we experimentally assess how herbivore habitat selection and foraging, winter snowpack and their interactions influence the recruitment of aspen in Yellowstone National Park, USA.

Aspen is an ideal species for investigating the direct and indirect effects of climate change on population performance. It is an ecologically important tree species [14] that is in widespread decline across much of the US northern Rocky Mountains [15] owing to recruitment failure in the face of intense elk herbivory [16], possibly in combination with climatic factors [15]. Indeed, aspen demography is affected directly by both climate [17,18] and elk herbivory [16], while elk themselves may be affected by climate change-altered snowpack conditions [13]. Elk browse on woody shrubs in the winter while during the growing season they are grazers. Elk winter distribution is known to be constrained by deep snow [19,20]. Snowpack declined significantly in northern Yellowstone over the latter half of the twentieth century ([21]; also see the electronic supplementary material). But whether changing snow conditions affect browsing rates [22] or plant demography and persistence remains unclear. No study has yet

* Author for correspondence (jedediah.brodie@gmail.com).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.1501> or via <http://rspb.royalsocietypublishing.org>.

experimentally addressed the interplay between snow and herbivory on plant demography. We focus here on ramet rather than genet demography since generation of new aspen stems in our study region is almost entirely through clonal (asexual) sprouting rather than seedling establishment [15].

2. METHODS

We stratified the winter range of the northern Yellowstone elk herd (approx. 1500 km²; 1500–2000 m elevation) into approximately equal-sized sub-units and randomly chose aspen stands within each stratum in autumn 2007, for a total of 104 stands. At most of these stands, we marked five randomly selected aspen vegetative suckers with unique identification tags. At a subset of 10 aspen stands, we marked individual suckers within six clusters (usually approx. six to eight suckers per cluster) and built wire ungulate exclosures over three clusters at each site in early November (autumn) of each year, removing the exclosures in late May (spring). We measured the height and the survival of all suckers in autumn 2007, spring 2008, autumn 2008 and spring 2009. When suckers died, new suckers were marked to keep the total number of tagged suckers constant at each site.

We used the Langur snow model [23,24] to predict the peak snow water equivalent (SWE) at each site during each winter. SWE integrates snowpack depth and density and is an important predictor of ungulate behaviour and movement in winter (cf. [19,20]). Langur represents daily snowpack accumulation and ablation across a spatially heterogeneous landscape. Precipitation and temperature inputs are interpolated from nearby climate-measuring stations, and spatial drivers of snowpack variation such as forest cover and wind exposure are derived from topographic mapping and Landsat remote sensing estimates [25]. The model was validated against a random sample of snowpack measurements throughout Yellowstone by Watson *et al.* [23].

We used camera traps to assess elk usage of sites as a function of SWE. We deployed cameras at a subset of 17 of the aspen demography sites in 2007–2008 and 19 sites in 2008–2009. Sites were haphazardly chosen to straddle a gradient in snowpack, but with no prior knowledge of site-specific browsing rates or elk usage. We used Reconyx RM45 camera traps that were active 24 h a day. We assessed the daily probability of site visitation by elk as a function of daily predicted SWE using logistic regression, controlling for within-site correlations using a clustered variance design [26].

We assessed winter (1 November–31 May), summer (1 June–31 October) and annual (1 November–31 October) sucker growth using general linear models (GLMs) and annual survival using logistic regression survival analysis. We used the following predictor variables in all models: *sucker height* (cm), predicted maximum SWE (cm) averaged over a 100 m radius from the centroid of the site, SWE², *exclosure* (binary) and an SWE × *exclosure* interaction term. Quadratic SWE terms were included because data from other systems suggest that plant productivity can peak at intermediate snowpack levels [12]. For sucker growth, the sampling unit was mean height change at a given site, whereas the survival analysis was conducted at the level of individual suckers; however, we used a clustered variance design to account for within-stand correlations in vital rates [26]. We used backward-elimination stepwise regression to ascertain which predictor variables significantly affected

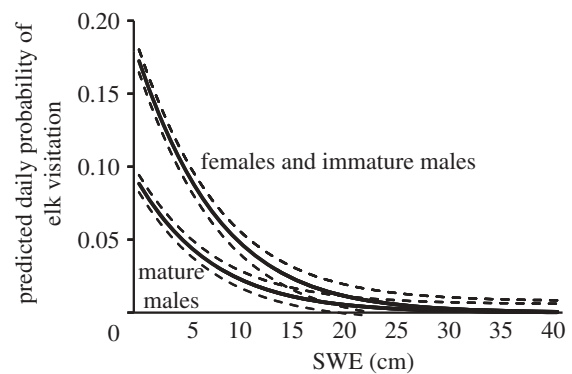


Figure 1. Predicted daily probability of elk visitation to aspen stands.

growth and survival, with a cut-off for removal from the model of $p \geq 0.05$.

We also estimated the site-specific probability of suckers recruiting to the ‘less-browsable height’ of 200 cm. Elk occasionally straddle and push over aspen stems even taller than this; yet, browsing is considerably reduced beyond the threshold of approximately 200 cm [16,27]. We estimated the annual probability of recruitment using the equation (from Crouse *et al.* [28]):

$$P_{\text{recruitment}} = \frac{(S^d)(1 - S)}{(1 - S^d)}, \quad (2.1)$$

where S is site-specific annual survival and d is the duration (in years) a sucker would stay in the ‘sucker’ stage class before reaching 200 cm; $d = 200/G$, where G is the site-specific annual growth rate in centimetre. We estimated the variance in $P_{\text{recruitment}}$ as a function of the variance in S and G using the delta method.

In our study on the effects of climate and herbivory on aspen, we did not assess the potentially confounding influence of wolves, which certain previous studies have suggested could alter elk browsing behaviour (e.g. [29]). Recent work showed no influence of spatial variation in wolf predation risk on aspen survival or growth in Yellowstone [16], and little influence of wolves on the broad-scale winter distribution of elk [20,30,31]. Likewise, elk browsing on willow in Yellowstone is more strongly affected by snow conditions than by wolves [32].

3. RESULTS

Over a total of 2434 camera-trap-days in the winter of 2007–2008 and 3214 trap-days in 2008–2009, the daily probability of sites being visited by elk declined significantly with increasing SWE (partial $p < 0.01$; figure 1). The daily probability of site visitation was also lower for mature male elk than for females and immature males combined ($p = 0.04$; figure 1). This difference is likely due to mature males being less abundant than other age/sex classes, rather than differential responses to snow, since the SWE × *male* interaction term was not significant.

Across 104 aspen stands, height change of vegetative suckers during winter was negative at nearly all sites due to ungulate browsing, but was positive during the summer (figure 2). SWE significantly reduced winter height loss from browsing (table 1), but also significantly reduced vertical height gains during the following summer by nearly the same magnitude, probably because longer

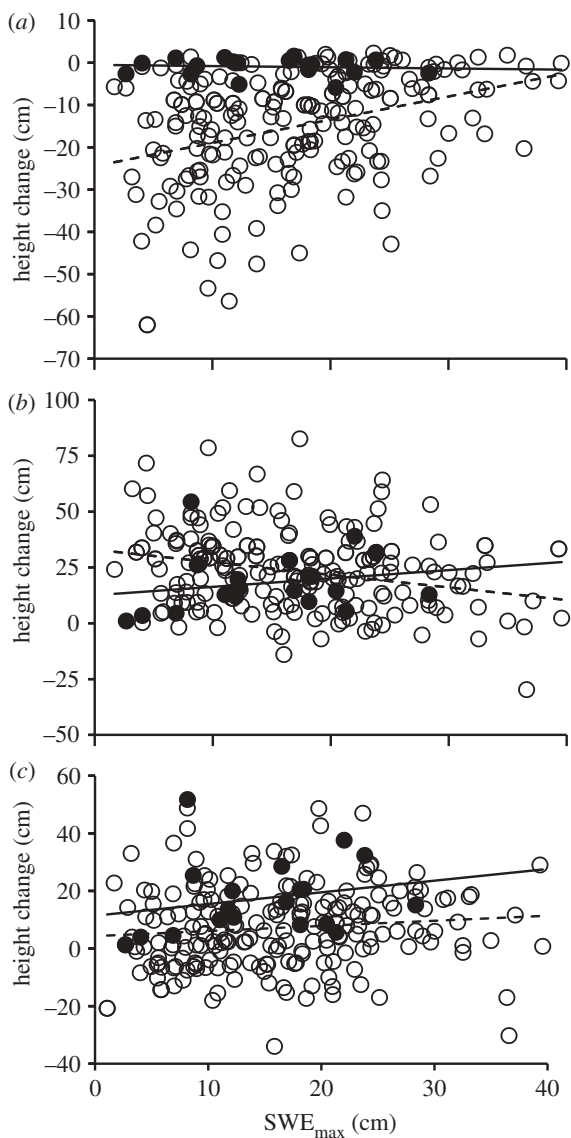


Figure 2. Average height change of aspen suckers versus maximum winter snow water equivalent (SWE) at each site. Open circles and dashed trendlines represent unprotected suckers, black circles and solid trendlines represent those inside wire enclosures during the winter. (a) Winter; (b) summer; (c) annual.

melt-times shorten the growing season for aspen suckers in areas with deep snow. As a result of these off-setting effects, SWE did not explain annual growth, which was significantly affected only by whether suckers had been protected from elk browsing during winter (table 1). Annual sucker survival was positively affected by SWE and the SWE \times enclosure interaction (table 1 and figure 3a).

While we experimentally manipulated herbivory, we relied on natural spatial variation in SWE to assess the influence of snowpack on aspen recruitment. Though SWE was correlated with *elevation* (see the electronic supplementary material), sucker survival data were much better fit by SWE as a predictor variable rather than *elevation* ($\Delta\text{AIC} = 14.14$; electronic supplementary material, table S1). Likewise, SWE was a far better predictor of sucker survival than were several other factors that varied spatially across the landscape, including *predation risk* (from [30]; $\Delta\text{AIC} = 18.61$), *forest canopy cover* ($\Delta\text{AIC} = 18.59$) and *ground cover height* ($\Delta\text{AIC} = 18.74$). Winter browsing rate

data were also much better fit by SWE than by *predation risk* ($\Delta\text{AIC} = 2.39$; electronic supplementary material, table S2). Annual recruitment probability (estimated from equation 2.1) was substantially higher inside enclosures and increased as a function of SWE (figure 3b).

4. DISCUSSION

This study demonstrates that the long-term decline of snowpack in northern Yellowstone may have helped reduce the prevalence of ideal conditions for aspen recruitment. While increased annual snowfall reduces growth rate of adult aspen [17], our data suggest that recruitment of vegetative suckers to less-browsable height classes is strongly enhanced by thick snowpack. Though snowpack has no net effect on annual sucker growth, thick snowpack reduces elk browsing pressure and enhances sucker survival, which increases recruitment probabilities (figure 3b). Climate change can affect aspen survival directly through impacting sucker survival, and indirectly by altering the strength of herbivory (figure 3a), but can also affect herbivore abundance. Indeed, though the elk population in northern Yellowstone itself has declined since the late 1990s [33], elk populations in many other localities in the Rocky Mountains are predicted to increase [13,34] owing to reduced winter snowpack across much of the western United States [35]. Thus, across the northern Rocky Mountain region, aspen recruitment could be precluded owing to more intense herbivory combined with changed abiotic conditions. Indeed, winters in northern Yellowstone are currently drier than they have been throughout much of the Holocene [36], and certainly more xeric than in the late 1800s and early 1900s [37] when many of the extant aspen stands in the area originated [16]. Conditions for aspen recruitment may thus face a future with few historical analogues under further climate change.

The impacts of herbivory on aspen are shaped by elk behavioural responses to snowpack. Though deep snow is known to drive elk to lower elevations [38], our results are the first to show that such distributional changes can affect the demography and persistence of plant populations. This could be an important mechanism by which climate change affects plant persistence, though one that has hitherto received very little attention. Changing snowpack conditions could also affect plants through altering nutrient and soil conditions or physical damage to stems [39].

Our study also reinforces that herbivory can strongly modify plant responses to climate change in general. Numerous studies have assessed how changing abiotic conditions could directly impact particular species through ecophysiological impacts (e.g. [40,41]). Yet, responses to climate change may be much more strongly determined by altered species interactions than by direct physiological responses (e.g. [2,5]). Our results suggest that, in the absence of browsing, reduced snowpack in the Rocky Mountains could lead to a substantial decline in aspen recruitment (figure 3). This impact is even greater when herbivory is considered; indeed, herbivory at current levels substantially limits recruitment.

Although herbivory and changing abiotic conditions are both likely to influence plant populations, herbivory may be the more important factor of the two. In our study, the

Table 1. Coefficients (with 95% CIs) from final models of stepwise regressions; all models and parameters are significant at $\alpha = 0.05$. All models started with *sucker height* (cm), snow water equivalent (SWE; in cm), SWE^2 , enclosure (binary), and an $SWE \times enclosure$ interaction term. Column headings and underlined sub-headings indicate independent and dependent variables, respectively.

<u>height</u>	<u>SWE</u>	<u>enclosure</u>	<u>SWE \times enclosure</u>	<u>constant</u>
<i>winter height change</i>	0.46 (0.25, 0.66)	14.88 (11.96, 17.81)		-13.86 (-19.91, -7.81)
<i>summer height change</i>	-0.48 (-0.87, -0.10)			30.94 (23.36, 38.52)
<i>annual height change</i>		10.16 (4.33, 15.99)		7.18 (5.29, 9.06)
<i>annual survival</i>	0.03 (0.01, 0.06)		0.05 (0.01, 0.08)	

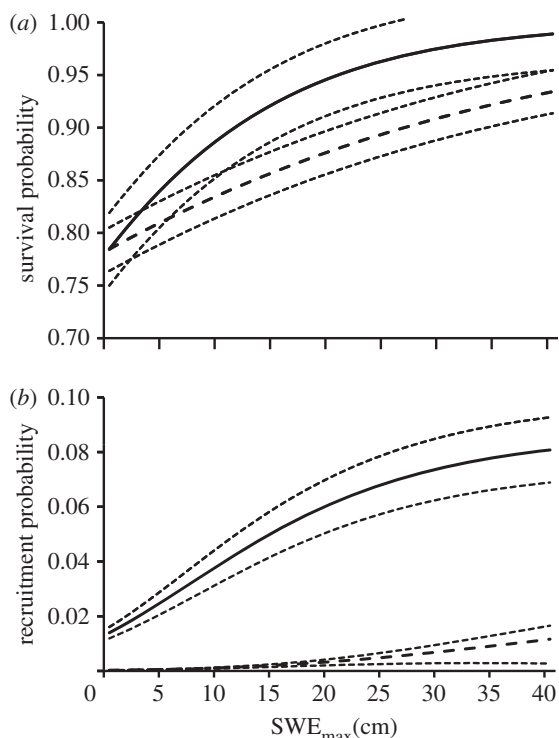


Figure 3. (a) Annual survival and (b) recruitment probability from equation (2.1) of aspen suckers versus maximum winter SWE for unprotected suckers (dashed line, 95% confidence limits) and suckers inside wire enclosures (solid line).

influence of herbivory on recruitment is stronger than the influence of reduced snowpack. Likewise, the abundance of mosses and shrubs in a high arctic ecosystem on Spitsbergen Island was also more strongly driven by herbivores than by warming temperatures [42]. Thus, the indirect impacts of climate change (altered trophic interactions) may be stronger than the direct effects, highlighting the importance of incorporating species interactions into climate change prediction efforts.

We thank the staff of Yellowstone National Park for research permits and assistance, particularly C. Hendrix, D. Smith, P. J. White and R. Renkin. We are also indebted to O. Helmy, C. Brant, M. Tercek, I. Brant and others for fieldwork and assistance. This work was funded by a David H. Smith Conservation Research Fellowship, supported by the Society for Conservation Biology and the Cedar Tree Foundation, to J. Brodie. We are also grateful to J. Maron, T. Martin, M. Kauffman and E. Jules for helpful comments on the manuscript.

REFERENCES

- 1 Post, E., Brodie, J., Hebblewhite, M., Anders, A. D., Maier, J. A. K. & Wilmsers, C. C. 2009 Global population dynamics and hotspots of response to climate change. *BioScience* **59**, 489–497. (doi:10.1525/bio.2009.59.6.7)
- 2 Suttle, K. B., Thomsen, M. A. & Power, M. E. 2007 Species interactions reverse grassland responses to changing climate. *Science* **315**, 640–642. (doi:10.1126/science.1136401)
- 3 Kelly, A. E. & Goulden, M. L. 2008 Rapid shifts in plant distribution with recent climate change. *Proc. Natl Acad. Sci. USA* **105**, 11 823–11 826. (doi:10.1073/pnas.0802891105)
- 4 Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C. & Beissinger, S. R. 2008 Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264. (doi:10.1126/science.1163428)
- 5 Post, E. & Pedersen, C. 2008 Opposing plant community responses to warming with and without herbivores. *Proc. Natl Acad. Sci. USA* **105**, 12 353–12 358. (doi:10.1073/pnas.0802421105)
- 6 Martin, T. E. 2007 Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology* **88**, 367–380. (doi:10.1890/0012-9658(2007)88[367:CCOYOT]2.0.CO;2)
- 7 Heikkinen, R. K., Luoto, M., Virkkala, R., Pearson, R. G. & Korber, J. H. 2007 Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.* **16**, 754–763. (doi:10.1111/j.1466-8238.2007.00345.x)
- 8 Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J. C., Thuiller, W., Araujo, M. B., Guisan, A. & Zimmermann, N. E. 2010 Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* **33**, 1038–1048. (doi:10.1111/j.1600-0587.2010.06229.x)
- 9 Pellissier, L. *et al.* 2010 Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography* **33**, 1004–1014. (doi:10.1111/j.1600-0587.2010.06386.x)
- 10 Schmitz, O. J., Post, E., Burns, C. E. & Johnston, K. M. 2003 Ecosystem responses to global climate change: moving beyond color mapping. *Bioscience* **53**, 1199–1205. (doi:10.1641/0006-3568(2003)053[1199:ERTG CC]2.0.CO;2)
- 11 Post, E., Peterson, R. O., Stenseth, N. C. & McLaren, B. E. 1999 Ecosystem consequences of wolf behavioural response to climate. *Nature* **401**, 905–907. (doi:10.1038/44814)
- 12 Forchhammer, M. C., Post, E., Berg, T. B. G., Høye, T. T. & Schmidt, N. M. 2005 Local-scale and short-term herbivore-plant spatial dynamics reflect influences

- of large-scale climate. *Ecology* **86**, 2644–2651. (doi:10.1890/04-1281)
- 13 Creel, S. & Creel, M. 2009 Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error. *J. Anim. Ecol.* **78**, 1291–1297. (doi:10.1111/j.1365-2656.2009.01581.x)
 - 14 DeByle, N. V. 1985 Wildlife. In *Aspen: ecology and management in the western United States* (eds N. V. DyByle & R. P. Winokur), Washington, DC: US Department of Agriculture Forest Service General Technical Report RM-119.
 - 15 Romme, W. H., Turner, M. G., Wallace, L. L. & Walker, J. S. 1995 Aspen, elk and fire on the northern range of Yellowstone National Park. *Ecology* **76**, 2097–2106. (doi:10.2307/1941684)
 - 16 Kauffman, M. K., Brodie, J. F. & Jules, E. 2010 Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* **91**, 2742–2755. (doi:10.1890/09-1949.1)
 - 17 Brown, K., Hansen, A. J., Keane, R. E. & Graumlich, L. J. 2006 Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. *Landscape Ecol.* **21**, 933–951. (doi:10.1007/s10980-005-6190-3)
 - 18 Rehfeldt, G. E., Ferguson, D. E. & Crookston, N. L. 2009 Aspen, climate, and sudden decline in western USA. *Forest Ecol. Manag.* **258**, 2353–2364. (doi:10.1016/j.foreco.2009.06.005)
 - 19 Proffitt, K. M., Gude, J. A., Hamlin, K. L., Garrott, R. A., Cunningham, J. A. & Grigg, J. L. 2011 Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *J. Appl. Ecol.* **48**, 471–478. (doi:10.1111/j.1365-2664.2010.01928.x)
 - 20 White, P. J., Garrott, R. A., Cherry, S., Watson, F. G. R., Gower, C. N., Becker, M. S. & Meredith, E. 2009 Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. In *The ecology of large mammals in central Yellowstone* (eds R. A. Garrott, P. J. White & F. G. R. Watson), pp. 451–476. Amsterdam, The Netherlands: Elsevier.
 - 21 Wilmers, C. C. & Getz, W. M. 2005 Gray wolves as climate change buffers in Yellowstone. *PLoS Biol.* **3**, e92. (doi:10.1371/journal.pbio.0030092)
 - 22 Forester, J. D., Anderson, D. P. & Turner, M. G. 2007 Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (*Populus tremuloides* Michx.) in Yellowstone National Park (USA)? *Forest Ecol. Manag.* **253**, 211–219. (doi:10.1016/j.foreco.2007.07.019)
 - 23 Watson, F. G. R., Anderson, T. N., Newman, W. B., Cornish, S. S. & Thien, T. 2009 Modeling spatial snowpack dynamics. In *The ecology of large mammals in central Yellowstone* (eds R. A. Garrott, P. J. White & F. G. R. Watson), pp. 85–112. Amsterdam, The Netherlands: Academic Press.
 - 24 Watson, F. G. R., Newman, W., Coughlan, J. C. & Garrott, R. A. 2006 Testing a distributed snowpack simulation model against diverse observations. *J. Hydrol.* **328**, 453–466. (doi:10.1016/j.jhydrol.2005.12.012)
 - 25 Watson, F. G. R. & Newman, W. B. 2009 Mapping mean annual precipitation using trivariate kriging. In *The ecology of large mammals in central Yellowstone* (eds R. A. Garrott, P. J. White & F. G. R. Watson), pp. 37–52. Amsterdam, The Netherlands: Academic Press.
 - 26 Cleves, M., Gutierrez, R. G., Gould, W. & Marchenko, Y. V. 2010 *An introduction to survival analysis using Stata*. College Station, TX: Stata Press.
 - 27 Kay, C. E. 1990 *Yellowstone's northern elk herd: a critical evaluation of the 'natural-regulation' paradigm*. PhD Dissertation, Utah State University, Logan, Utah
 - 28 Crouse, D. T., Crowder, L. B. & Caswell, H. 1987 A stage-based population-model for loggerhead sea turtles and implications for conservation. *Ecology* **68**, 1412–1423. (doi:10.2307/1939225)
 - 29 Ripple, W. J., Larsen, E. J., Renkin, R. A. & Smith, D. W. 2001 Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol. Conserv.* **102**, 227–234. (doi:10.1016/S0006-3207(01)00107-0)
 - 30 Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. & Boyce, M. S. 2007 Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecol. Lett.* **10**, 690–700. (doi:10.1111/j.1461-0248.2007.01059.x)
 - 31 Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M. & Merrill, E. H. 2005 Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *J. Wildl. Manag.* **69**, 1691–1707. (doi:10.2193/0022-541X(2005)69[1691:HSBE BA]2.0.CO;2)
 - 32 Creel, S. & Christianson, D. 2009 Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* **90**, 2454–2466. (doi:10.1890/08-2017.1)
 - 33 Eberhardt, L. L., White, P. J., Garrott, R. A. & Houston, D. B. 2007 A seventy-year history of trends in Yellowstone's northern elk herd. *J. Wildl. Manag.* **71**, 594–602. (doi:10.2193/2005-770)
 - 34 Wang, G. M., Hobbs, N. T., Singer, F. J., Ojima, D. S. & Lubow, B. C. 2002 Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, USA. *Climatic Change* **54**, 205–223. (doi:10.1023/A:1015725103348)
 - 35 Mote, P. W., Hamlet, A. F., Clark, M. P. & Lettenmaier, D. P. 2005 Declining mountain snowpack in western North America. *Bull. Am. Meteorol. Soc.* **86**, 39–49. (doi:10.1175/BAMS-86-1-39)
 - 36 Whitlock, C. & Bartlein, P. J. 1993 Spatial variations of Holocene climatic-change in the Yellowstone region. *Quat. Res.* **39**, 231–238. (doi:10.1006/qres.1993.1026)
 - 37 Whitlock, C., Dean, W., Rosenbaum, J., Stevens, L., Fritz, S., Bracht, B. & Power, M. 2008 A 2650-year-long record of environmental change from northern Yellowstone National Park based on a comparison of multiple proxy data. *Quat. Int.* **188**, 126–138. (doi:10.1016/j.quaint.2007.06.005)
 - 38 White, P. J. & Garrott, R. A. 2005 Northern Yellowstone elk after wolf restoration. *Wildl. Soc. Bull.* **33**, 942–955. (doi:10.2193/0091-7648(2005)33[942:NYE AWR]2.0.CO;2)
 - 39 Jones, H. G., Pomeroy, J. W., Walker, D. A. & Hoham, R. W. 2001 (ed.) *Snow ecology: an interdisciplinary examination of snow-covered ecosystems*. Cambridge, UK: Cambridge University Press.
 - 40 Briones, M. J. I., Ineson, P. & Heinemeyer, A. 2007 Predicting potential impacts of climate change on the geographical distribution of enchytraeids: a meta-analysis approach. *Global Change Biol.* **13**, 2252–2269. (doi:10.1111/j.1365-2486.2007.01434.x)
 - 41 Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C. & Longino, J. T. 2008 Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258–261. (doi:10.1126/science.1162547)
 - 42 Gornall, J. L., Woodin, S. J., Jonsdottir, I. S. & van der Wal, R. 2009 Herbivore impacts to the moss layer determine tundra ecosystem responses to grazing and warming. *Oecologia* **161**, 747–758. (doi:10.1007/s00442-009-1427-5)