

Climate impacts on bird and plant communities from altered animal-plant interactions

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The contribution of climate change to declining populations of organisms remains a question of outstanding concern¹⁻³. Much attention to declining populations has focused on how changing climate drives phenological mismatches between animals and their food⁴⁻⁶. Effects of climate on plant communities may provide an alternative, but particularly powerful, influence on animal populations because plants provide their habitats. Here, we show that abundances of deciduous trees and associated songbirds have declined with decreasing snowfall over 22 years of study in montane Arizona, USA. We experimentally tested the hypothesis that declining snowfall indirectly influences plants and associated birds by allowing greater over-winter herbivory by elk (*Cervus canadensis*). We excluded elk from one of two paired snowmelt drainages (10 ha per drainage), and replicated this paired experiment across three distant canyons. Over six years, we reversed multi-decade declines in plant and bird populations by experimentally inhibiting heavy winter herbivory associated with declining snowfall. Moreover, predation rates on songbird nests decreased in enclosures, despite higher abundances of nest predators, demonstrating the over-riding importance of habitat quality to avian recruitment. Thus, our results suggest that climate impacts on plant-animal interactions can have forceful ramifying effects on plants, birds, and ecological interactions.

One of the clearest signals of anthropogenically driven climate change is the declining snowfall observed across mountains of the world^{1,7,8}. Reductions in winter snowpack can influence the abundance and growth of individual tree species^{9,10}, and changes in the plant community may then impact populations of animals that rely on these plants for habitat. As most animals, including breeding songbirds, have specific habitat requirements¹¹, changes in habitat through plant responses to climate change have great potential to influence entire bird communities. Climate-driven change in plant communities can also influence the abundance and search efficiency of avian nest predators¹¹. Thus, climate change may indirectly affect songbird abundance via trophic (predation) as well as non-trophic (habitat) routes. These varied impacts of climate change on bird assemblages remain unstudied.

Declining snowfall can influence plant communities by either negatively influencing plant demographics^{12,13}, or by changing plant-herbivore interactions. Large ungulates are dominant herbivores in many high-elevation and high-latitude systems and can strongly influence plant productivity and demography^{14,15}. Declining snowfall has great potential to influence plant communities indirectly if it alters interactions between ungulates and plants. Here, we demonstrate that reduced snowfall mediates

dramatic shifts in plant and bird communities, as well as predation on bird nests, through increased herbivory by elk, a dominant ungulate herbivore.

Snowfall at our study area has declined over the past 25 years (Fig. 1a), typical of what has occurred across western North America and other mountain regions of the world^{1,7,8}. Major long-term decreases in stem densities of deciduous woody plants (Fig. 1b) were strongly associated with snowfall across the previous three winters (Fig. 1c), even when based on detrended time series analyses (see Supplementary Statistical Analyses). Snowfalls in the three winters were not correlated with each other, but each year contributed highly significant independent and additive effects that together accounted for 85% of the decline in plant densities (Fig. 1c, Supplementary Statistical Analyses). The significant contributions of three uncorrelated years of snowfall to explaining plant densities cannot occur by chance and together with the extensive total variation explained (Fig. 1c) indicate a causal role of snow on deciduous woody plant densities. The effects of snow over the previous three winters makes clear biological sense because plant density is influenced by density and recruitment in earlier years, such that impacts of snow on density and recruitment in one year will affect densities in future years (Fig. 1).

The visually dramatic decline in plant densities from 1985 to 2011 occurred even though regional elk abundances were generally declining (Fig. 1d-f). The decline in deciduous woody plants, in turn, was associated with changing abundances of six species of songbirds that nest on the ground or in the forest understory; five of the six species showed declining populations with the decline in vegetation (Fig. 2a; also see Supplementary Table S1). These reductions in songbird populations were not reflected in regional population trends (see Supplementary Table S2), demonstrating that our results were not driven by extrinsic broader-scale influences on populations. The causal mechanisms by which changing snow underlies these long-term trends in birds and plants in our study system have been unclear. However, understanding these causal mechanisms has broad implications because snowpack continues to decline in mountainous areas worldwide^{1,7,8}.

The worldwide decline in snow^{1,7,8} could have important direct influences on plants by reducing deep-soil water that can affect plant demography, especially the deciduous woody species on our site^{12,13}. Moreover, an associated worldwide decline in evapotranspiration¹⁶ might explain the decline in birds, as evapotranspiration strongly correlates with the ecosystem productivity that underlies abundances and diversity of birds and other taxa^{17,18}. These effects potentially represent direct 'bottom-up' impacts of climate on ecosystems. Furthermore, snow can also influence the distribution and impacts of large herbivores, which

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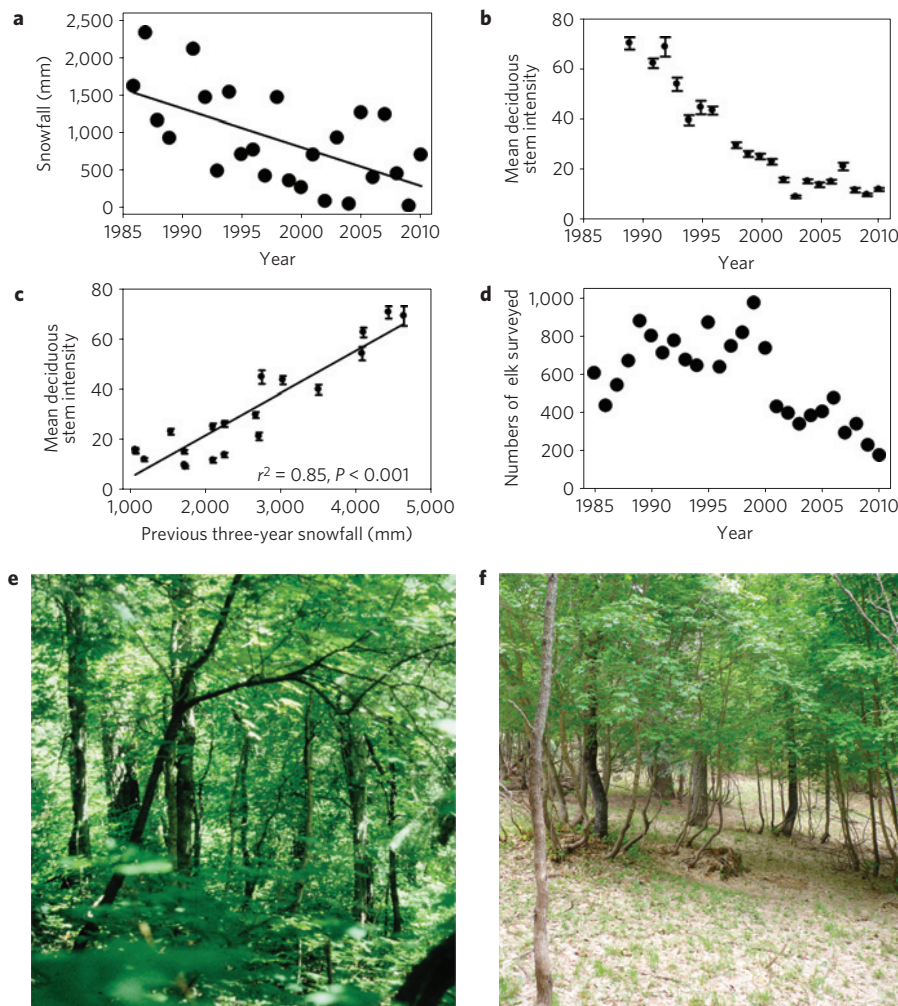


Figure 1 | Long-term declines in total snowfall, deciduous woody plants and elk. **a,b**, Total snowfall (October–March) (**a**), and mean (\pm s.e.m.) density of deciduous woody plant stems (number of stems >25 cm tall in 5 m radius samples, $N = 313$ –535 samples yr^{-1}) (**b**), declined across years. **c**, Relative densities of deciduous stems were strongly correlated with additive effects of snowfall over the previous three winters (see Supplementary Statistical Analyses). **d**, Numbers of elk surveyed for the region that includes winter and summer ranges (see Supplementary Methods) surrounding our study area. **e,f**, Photos showing the decline in understory plant density in the same area of a study drainage from May 1985 (**e**) to May 2011 (**f**).

might have ‘top-down’ effects. Accumulation of even minimal depths of snow causes rapid increases in the energy costs of movement for elk, often driving them to lower elevations^{19–22}. This occurs in our study area; radio-collared elk move to lower elevations during periods of greater snowfall²². Such shifts in winter distributions are important because elk primarily browse on woody plants in winter²⁰ and shifts in distributions due to snow affects the browsing pressure on tree recruitment²¹. Long-term declines in the abundances of woody plants on our study site (Fig. 1b), therefore, could result from the direct effects of decreasing snow on soil water or indirectly through snow impacts on elk herbivory. Similarly, the long-term population changes of birds might reflect the direct effects of snow on ecosystem productivity and phenology^{4–6,16–18}, or indirect effects through changing plant densities. To separate these alternatives, in autumn 2004 we constructed large-scale (10 ha) elk exclosures surrounding entire drainages. We paired these exclosures with adjacent control drainages of similar size and orientation. We replicated this paired design across three sites, which were 2–5 km apart and separated by deep canyons. Exclosures should have minimal influence on plant densities if the bottom-up effect of snow water is most important, whereas plant densities should increase in exclosures compared with control drainages if the top-down effect of elk herbivory is most important.

Exclusion of elk resulted in rapid increases in the density of young deciduous woody plants (Fig. 3a). Indeed, as a measure of how strongly plants responded to elk exclusion, plant densities in exclosures in 2010 were equivalent to those last observed on control plots in 1994–1996 (Fig. 1b), indicating that suppression of elk herbivory quickly reversed 15 years of plant density decline. The height of permanently marked ramets and seedlings of the major deciduous woody plant species also increased strongly with time within elk exclosures, whereas marked individuals showed little change in height on control drainages owing to continued browsing pressure (Fig. 3b). After six years of growth inside exclosures, aspen (*Populus tremuloides*) has begun to reach a height (as much as 5 m for some plants) where it would escape from elk browsing without exclosures. Thus, both the density and height of deciduous woody plants dramatically increased in exclosures compared with control drainages, a change that is visually striking (Fig. 3c,d). The insight of this experimental result is that it clearly rules out the direct effects of snowfall in driving increases in woody vegetation (Fig. 3) given that exclosure and control plots received the same snowfall. Rather, the causal driver of plant change is elk herbivory, with the strength of the elk–plant interaction being modified by long-term declining snowfall.

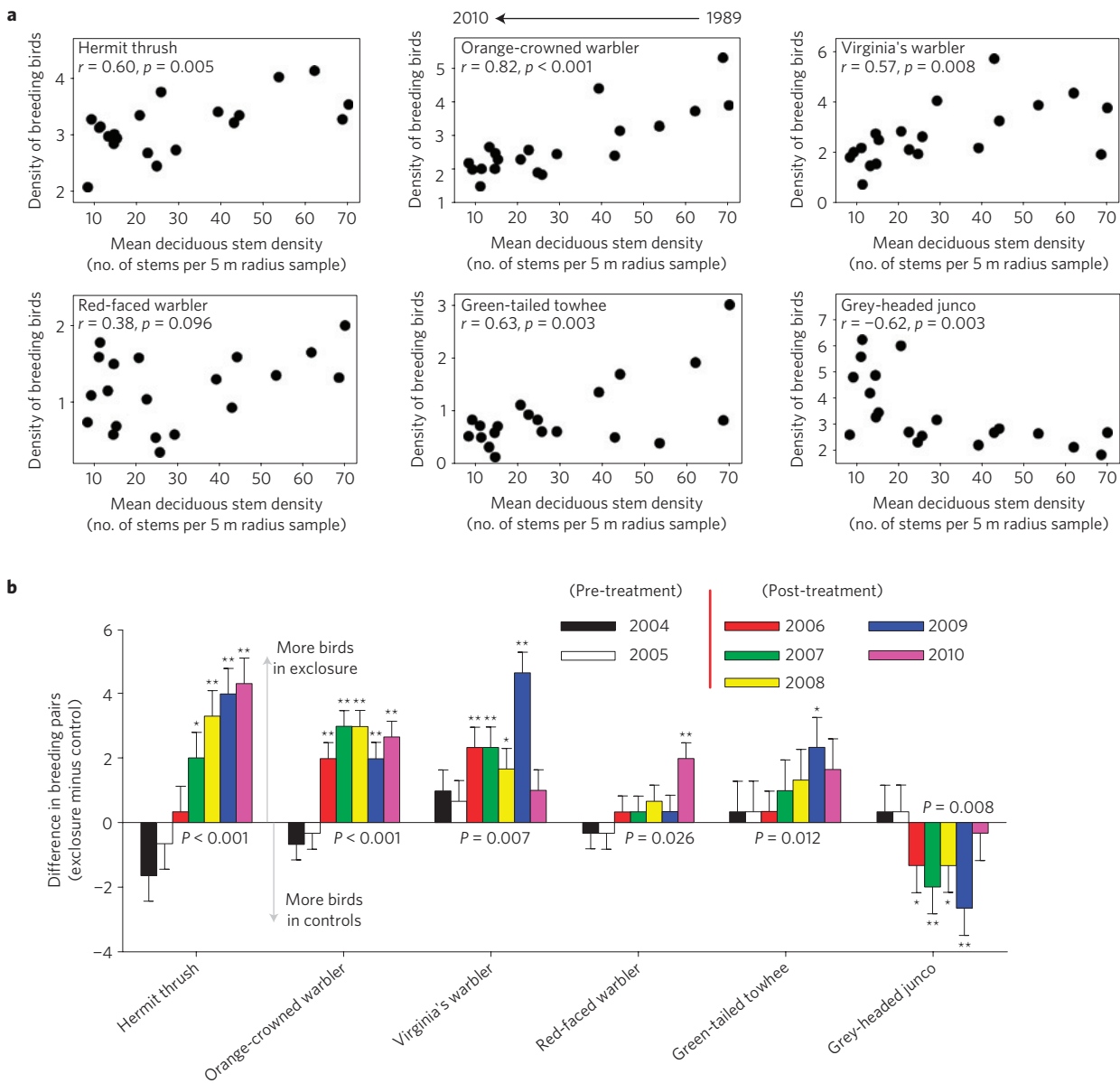


Figure 2 | Densities of breeding birds (number of breeding pairs per 10 ha drainage) over time and between treatments. a, Long-term changes in breeding densities of six bird species were correlated with the decline in density of deciduous woody plants (Fig. 1b, Supplementary Table S1). Note that the lowest plant densities reflect the most recent years. **b**, Mean differences (\pm s.e.m.) in breeding bird densities for exclosures minus controls ($N = 3$). Positive differences reflect higher densities on exclosure drainages and negative differences reflect the opposite. Asterisks ($*P < 0.075$, $**P < 0.05$) show differences between treatments in individual years. P -values test whether treatment differences changed from pre-treatment (first two years when vegetation did not differ— Fig. 3a) to post-treatment periods (Supplementary Table S3).

The clear impacts of elk on plant densities and the strong correlation of plant densities with snowfall (Fig. 1c) could theoretically be explained if elk population sizes increased across years as snowfall declined. However, elk population sizes in the region at large (see Supplementary Information) have not increased as snow declined (Fig. 1a,d). Instead, elk populations have strongly declined over the past 11 years when snow has been relatively low (Fig. 1a,d). These regional numbers are based on a large area that encompasses both summer range (our study area and surrounding areas) and winter range (our study area and lower elevations). This regional population size does not reflect the number of elk overwintering on our study area but instead reflects the number of animals that are potentially available to create overwinter browsing impacts. The actual overwinter browsing impact, however, depends on the influence of snow on the overwinter presence of elk.

For example, even when elk population sizes for this region are high, the overwinter browsing impact can remain quite low if there is high snowfall. Deeper snow causes elk to move to lower elevations, as documented for both our study area²² and other geographic areas^{19–21}. This latter point is emphasized by the lack of recovery of plants in the past 11 years, when elk numbers were a fraction of earlier numbers (Fig. 1d) but snow levels remained relatively low (Fig. 1a) and allowed elk to stay in the area and browse overwinter. Yet, these trees clearly can recover quickly when herbivory is experimentally reduced (Fig. 3). These results emphasize that declining snow levels (Fig. 1a) and their influence on overwinter browsing pressure can have more powerful influences on plant communities than can changes in elk population sizes.

The five bird species that declined with woody plants over the long-term (Fig. 2a) exhibited higher densities within fenced versus

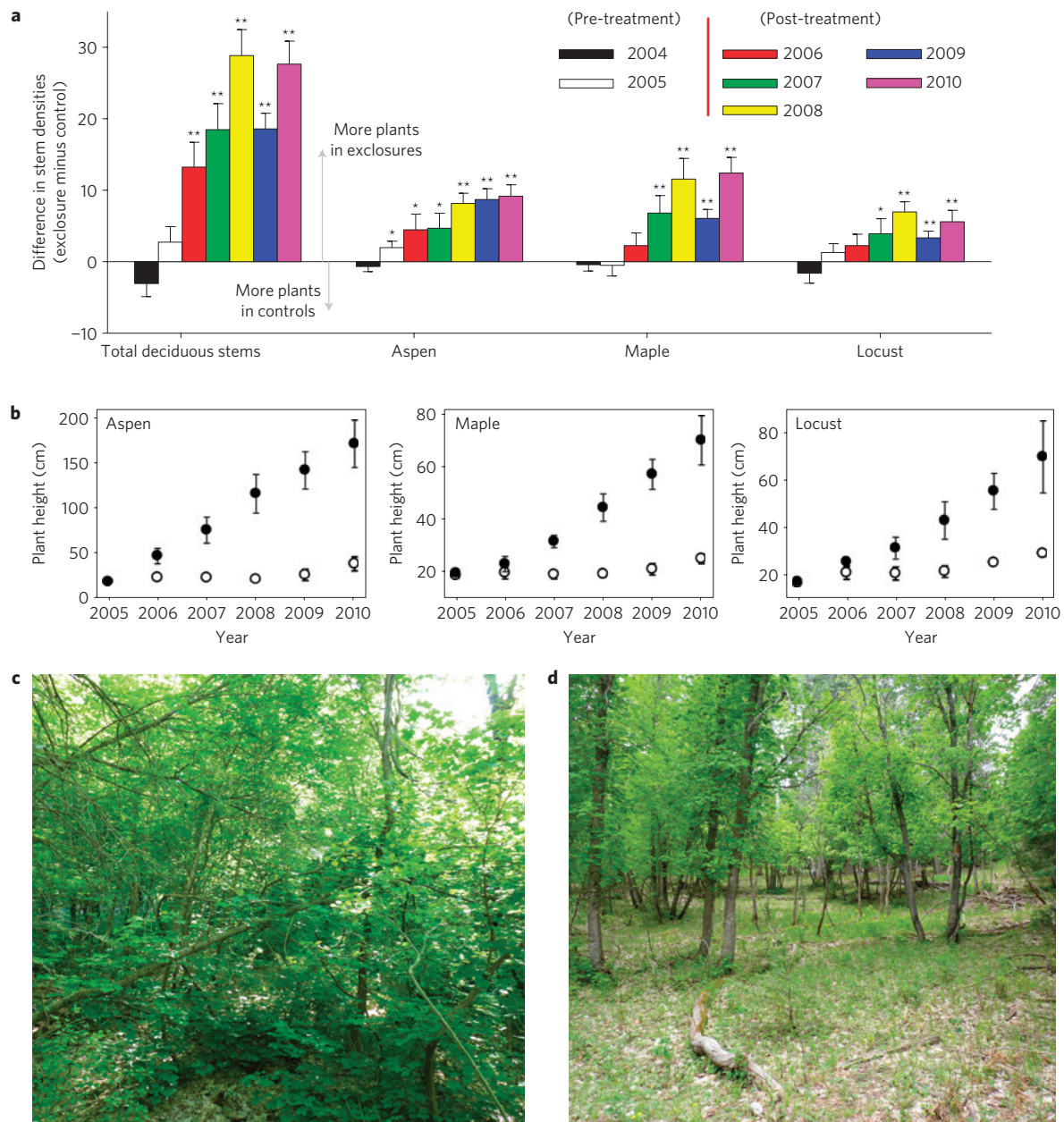


Figure 3 | Effects of elk exclusion on deciduous woody plant recruitment. **a**, Differences between paired enclosure minus control drainages in density (stems per 5 m radius sample, $N = 130\text{--}135$ samples yr^{-1}) of deciduous woody plants. Asterisks ($*P < 0.05$, $**P < 0.01$) show differences between treatments in individual years. Positive differences reflect higher densities on enclosures than control drainages that increased over time (Supplementary Table S4). **b**, Mean (\pm s.e.m.) height of individually marked woody plant species became substantially taller on enclosure than control drainages (Supplementary Tables S5, S6). **c,d**, Photos showing the much greater density of deciduous woody plants on an enclosure (**c**) versus paired control (**d**) drainage at the same general location on both drainages on 2 June 2011.

control drainages (Fig. 2b). The one bird species (grey-headed junco) that increased over the long-term (Fig. 2a) prefers open habitat²³ and it decreased in abundance in elk-excluded drainages (Fig. 2b) as the habitat rapidly filled in. In short, long-term changes in the densities of six bird species that were associated with the decline in deciduous woody plants (Fig. 2a) were abruptly reversed on enclosures (Fig. 2b) where deciduous plants increased (Fig. 3). These experimental results verify the causal influence of change in deciduous woody plant densities on breeding bird densities.

Abundances of breeding birds result from habitat selection and recruitment through reproductive success^{11,24}. Nest predation is commonly the primary limit on reproductive success¹¹, and

increased nest predation rates are often associated with decreased bird population sizes the following year^{24–26}. Small mammals, especially red squirrels (*Tamiasciurus hudsonicus*), grey-necked chipmunks (*Tamias cinereicollis*) and *Peromyscus* mice (to a much lesser extent), act as major nest predators in our system^{23,24}. The abundance of these predators together increased in enclosures relative to control drainages²⁷. Both increased abundances of nest predators and density-dependent responses to increased nest density can increase rates of nest predation^{11,28,29}. The higher densities of both predators²⁷ and nests (Fig. 2b) inside enclosures might, therefore, increase nest predation rates. Alternatively, increased vegetation density in enclosures (Fig. 3a) might reduce nest predation risk^{11,23}, potentially reversing long-term increases

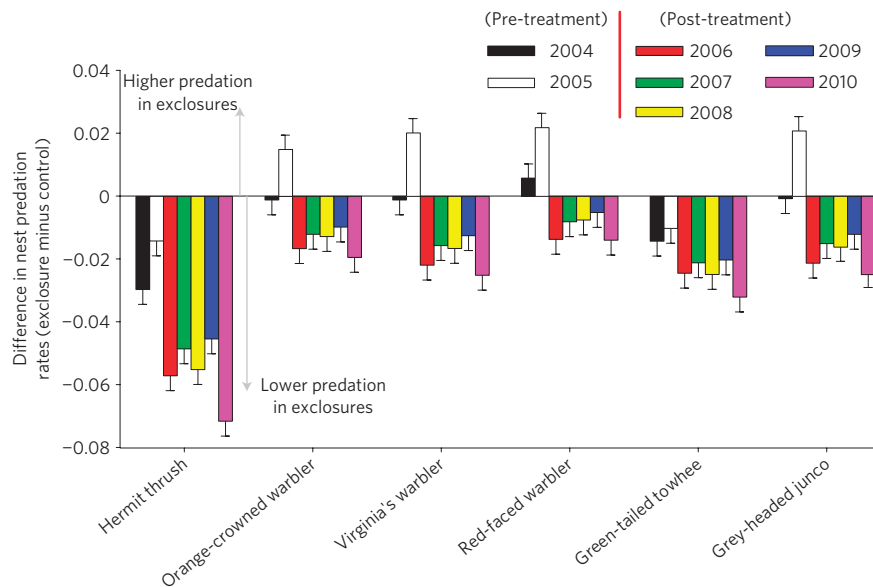


Figure 4 | Difference in daily nest predation rates (percentage of nests depredated daily) on enclosure minus control drainages across all species and years of study. Mean (\pm s.e.m.) nest predation rates ($N=1,643\text{--}7,016$ exposure days, 145–635 nests per species) did not differ between treatments during the pre-treatment period (Supplementary Table S8) but were strongly reduced in enclosures during the post-treatment period (Supplementary Table S9).

in nest predation rates associated with declining woody plant densities in our system²⁴. The extent to which increased vegetation density and complexity might offset increases in the abundances of predators and nests on nest predation rates has been untested until now. We found that nest predation rates were consistently reduced in enclosures (Fig. 4). Thus, the increases in woody plant density (Fig. 3a) had a greater influence on nest predation rates than the increases in small mammal densities²⁷ and nest densities (Fig. 2b). Ultimately, long-term declines in bird abundances and long-term increases in nest predation rates²⁴ were reversed, despite more predators in enclosures, when the habitat was allowed to recover from elk browsing.

Exclusion of elk from 10 ha drainages yielded rapid increases in tree (Fig. 3) and bird abundances (Fig. 2), and reductions in nest predation rates (Fig. 4), that reversed multi-decadal trends, while also changing the abundances and community composition of small mammals²⁷. These results suggest that the indirect effects of climate change can be quite powerful when acting through changes in plants. Particularly noteworthy is the fact that herbivore impacts on vegetation were strong even though elk numbers were substantially lower over the past decade than in all previous years (Fig. 1). This underscores how reduced snowpack resulting from warming climate can magnify the strength with which even small numbers of elk can influence vegetation and hence the entire ecosystem.

Our results also highlight how influences of climate change that operate simultaneously through multiple routes can have reinforcing consequences for animal populations. Declining habitat quality owing to increased winter herbivory from declining snowfall affects settling decisions by migratory birds as well as nest predation rates. These dual processes act synergistically to decrease numbers. These synergistic impacts of climate change, acting through altered species interactions, are a potentially potent driver of community change and require increasing attention. The complex radiation of consequences to ecosystem structure and function that can occur as a result of climate impacts on dominant herbivores and their interactions with plants will be increasingly important to consider as managers grapple with how to set harvest limits and other management goals in a changing world.

Methods

Long-term study sites were 22 snowmelt drainages at 2,400 m elevation. Annual variation in snowfall was obtained from a nearby weather station (15–30 km away from individual drainages). Elk population sizes were obtained from models of elk-take and annual roadside and aerial surveys conducted each August by Arizona Game and Fish Department (unpublished data available at http://www.azgfd.gov/h_f/hunting_units_5a.shtml). Elk population sizes are the total number of elk for a broad region defined geographically by Arizona Game and Fish Department that encompasses both summer range (our study area and much broader surrounding areas) and winter range (our study area and lower elevations). Our study area encompasses only a small part of this broader area. Population size in this entire region does not reflect the number of elk overwintering on our study area but instead is best thought of as an index of the number of animals that are potentially available to create overwinter browsing impacts. The actual overwinter browsing impact, however, depends on the influence of snow on the overwinter presence of elk.

To examine the effects of elk herbivory, in autumn 2004 we selected paired treatment and control drainages (generally separated by approximately 300–500 m) and erected an elk enclosure around one randomly selected drainage of each pair. Drainage pairs were replicated across three canyons (roughly 2–5 km apart). The enclosures consisted of a 3-m-tall game fence with high tension wires above it. Fences started 0.3 m above ground level to allow the entry and exit of all animals except elk (see Supplementary Fig. S1). The fence inhibited mule deer (*Odocoileus hemionus*) movement, but did not completely exclude them because they used the 0.3 m ground-level opening to crawl in and out.

We focused on the six most abundant ground- and shrub-nesting songbird species on our study drainages (hermit thrush—*Catharus gustatus*, orange-crowned warbler—*Oreothlypis celata*, Virginia's warbler—*Oreothlypis virginiae*, red-faced warbler—*Cardellina rubrifrons*, green-tailed towhee—*Pipilo chlorurus*, and grey-headed juncos—*Junco hyemalis*). Individuals of all bird species were counted on the same ten drainages from mid-May to mid-June each year from 1985 to 2010 and on the six paired experimental treatment plots using plot-mapping. We standardized the bird abundance to numbers of pairs per 10 ha across all drainages. Drainages were searched for bird nests every year. Nests were located by following adults, and these nests were carefully monitored for clutch size, predation, starvation and fledging rates using standardized long-term protocols.

Starting in 1989 we counted numbers of woody stems >25 cm tall for each plant species in 5 m-radius sampling circles at stratified random sites across each drainage. On the paired control and enclosure drainages, we established ten transects with five permanently marked sampling circles per transect and roughly 50 sampling circles per drainage. Starting in 2005, we used numbered metal tags to permanently mark, on average, 3–5 randomly selected individual ramets of quaking aspen—*Populus tremuloides*, canyon maple—*Acer grandidentatum* and New Mexican locust—*Robinia neomexicana* within each 5 m radius sampling circle on each control and enclosure drainage. Each summer thereafter, these marked plants were censused and measured for height.

See Supplementary Information for full Methods and associated references.

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Author contributions

T.E.M. and J.L.M. designed the study. T.E.M. conducted bird censuses across all years. T.E.M. collected data on nest predation with the assistance of a large number of field assistants and J.L.M. collected data on plant densities and heights with the assistance of many field assistants. T.E.M. and J.L.M. analysed the data and wrote the paper.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at <http://www.nature.com/reprints>. Correspondence and requests for materials should be addressed to T.E.M.