Title: Sampling bias exaggerates a textbook example of a trophic cascade

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Abstract:

Understanding how wildland ecosystems respond to the loss and recovery of large predators is vital to decipher the forces that structure food webs and to guide the practice of ecosystem conservation, restoration, and rewilding. This is a major scientific challenge, however, because these large-scale, uncontrolled systems are difficult (or impossible) to sample properly. We show how a tradition of nonrandom sampling has confounded this understanding in a textbook system (Yellowstone National Park) where carnivore [wolf (*Canis lupus*)] recovery is often associated with a trophic cascade involving changes in herbivore [elk (*Cervus canadensis*)] behavior and density that promote plant regeneration. Long-term data indicate that a customary practice of sampling only the tallest young plants overestimated regeneration of aspen (*Populus tremuloides*) by a factor of 3-44 compared to random sampling. Our results demonstrate how seemingly minor departures from principled sampling can generate substantial misunderstandings about the strength of trophic cascades caused by large terrestrial predators.

Main Text

Much of the empirical information about trophic cascades (indirect effects of predators on plants and abiotic processes) derives from tractable systems that are variously small scale, aquatic, invertebrate, and captive[1,2]. Substantially less is known about trophic cascades in free-living vertebrate communities that span vast landscapes. One reason for this gap is that it is difficult and costly to measure such large, complex, and uncontrolled systems in accordance with fundamental principles of sampling design, including randomization, replication, and control of variation[3–5]. This challenge also means that inference about trophic cascades in large terrestrial ecosystems may be particularly prone to bias.

Concern about sampling bias is a core issue in the longstanding debate about the cascading effects of wolves reintroduced to Yellowstone National Park[5–10]. In this system, the trophic cascade hypothesis is that wolves (*Canis lupus*) scared away and (or) killed enough elk (*Cervus canadensis*) to allow various woody deciduous plants (*Populus* spp., *Salix* spp.) to recover from decades of unchecked herbivory. A primary support for this hypothesis is time series data showing annual decreases in herbivory and annual increases in plant height following the 1995-1997 wolf reintroduction[10–21]. An inverse relationship between herbivory and plant height is considered critical evidence of a wolf-elk-aspen trophic cascade because it demonstrates the mechanism connecting the lower two trophic levels: reduced herbivory increases plant growth, leading to escape from herbivory if plants grow tall[17,19]. The standard, though untested, assumption is that plants taller than 200 cm escape the reach of elk and survive to join the overstory. A persistent concern is that reports of decreased herbivory and increased plant height after wolf reintroduction are based on sampling designs that deviate from fundamental principles[7–10].

Nonrandom sampling, for example, underpins nearly every annual trend in herbivory and height of young aspen (*Populus tremuloides*) in Yellowstone National Park that has been credited to a cascading effect of wolves (Extended Data Table 1)[10–20]. In this case, nonrandom sampling involves measuring the three or five tallest young aspen within a stand. The rationale is that the tallest young aspen are "consistently identified", the first to "experience a reduction in browsing pressure", and a "leading edge indication of a broader shift in plant community dynamics"[19]. An underappreciated problem, however, is that selective sampling of the tallest young aspen may misrepresent trends in the population of young aspen at large. Specifically, nonrandom sampling may have overestimated changes in herbivory and plant height[10], and thus exaggerated a globally-significant example of a trophic cascade featured in many textbooks[22,23] and popular media[24,25].

We assessed the scope of this potential bias and its implications for understanding trophic cascades in large terrestrial ecosystems with data from a long-term study of young aspen in 113 plots distributed across 995-km^2 of northern Yellowstone National Park (Fig. 1). Each plot was a 1 m × 20 m belt transect situated randomly within an aspen stand that was itself randomly selected from an inventory of aspen stands. Herbivory (browsed or unbrowsed) and height of the leader stem (the tallest stem) of every aspen ≤ 600 cm were measured at the end of the growing season. Herbivory and height of the five tallest stems ≤ 600 cm growing anywhere within each sampled stand were also measured. Although most plots were measured nearly every year since 1999[26], we focused on data from 10 years (2007-2014, 2016-2017) in which sampled stands included measurements of stems in randomly selected plots ('random stems') and of stems that were the five tallest ('5T stems').

Frequency distributions of herbivory levels and heights of 5T stems did not match those of random stems (Fig. 2), confirming that characteristics of the tallest young aspen did not represent those of the general population. Low herbivory levels (≤ 20% stems browsed) and tall heights (>100 cm) were more frequent among 5T stems in 2007 (Fig. 2, A and B), and even more so in 2017 (Fig. 2, C and D). Assuming the population of random stems was representative of the population of young aspen at large, disparities between the distributions of random and 5T stems indicate that sampling of 5T stems yielded biased estimates of average herbivory and stem height.

To test if 5T sampling overestimated annual changes in herbivory and stem height, we pooled measurements of all stems across all years and tested if and how the effect of year on herbivory and stem height varied according to sampling method. We treated the individual stem as the unit of analysis, used generalized linear mixed models (GLMMs) with a binomial error distribution to analyze herbivory as the probability that a stem was browsed, and used linear mixed models with a normal error distribution to analyze log-transformed stem height. All models included random effects for stand identity and year to control for repeated measurements, unmeasured stand-related effects, and stand-specific variation in annual rates of change. To determine the extent that annual changes in herbivory and stem height differed between sampling methods, we tested for an interaction between year and a dummy variable for sampling method.

Models with a year × sampling method interaction fit the data significantly better than did models with only main effects for these variables (herbivory: χ_1^2= 134.60, $P < 0.001$; height: χ_1^2= 49.42, $P < 0.001$). The interaction term indicated that annual changes estimated via 5T sampling were 1.3-3.0 times greater than annual changes estimated via random sampling. Specifically, herbivory decreased 23%·year^{-1} for 5T stems [95% CI = (18%, 27%), $P < 0.001$] versus

85 7%·year^{-1} for random stems [95% CI = (2%, 13%), P = 0.007; Fig. 3A], and stem height
86 increased 8.6%·year^{-1} for 5T stems [95% CI = (7.4%, 9.8%), P < 0.001] versus 6.7%·year^{-1} for
87 random stems [95% CI = (5.6%, 7.9%), P < 0.001; Fig. 3B).

88 One reason for these discrepancies was that the sample of 5T stems was dominated by
89 stems that exceeded critical height thresholds beyond which herbivory *decreased* as stems grew
90 taller; stems below these thresholds were subject to higher levels of herbivory that *increased* as
91 stems grew taller (Fig. 3C). A confidence set of GLMMs ($\Delta AIC_c < 2$) indicated the height
92 threshold was 127-140 cm for 5T stems and 118-129 cm for random stems (Extended Data
93 Tables, 2, 3). The most parsimonious models in the set indicated that 5T stems had a threshold at
94 132 cm and random stems at 122 cm, and that each 1-cm increase beyond these thresholds
95 decreased herbivory of 5T stems by 2.6% (95% CI = 2.4%, 2.9%; P < 0.001) and of random
96 stems by 2.2% (95% CI = 2.1%, 2.4%; P < 0.001). Below these thresholds, each 1-cm increase
97 in height increased herbivory of random stems by 0.3% (95% CI = 0.1%, 0.4%; P = 0.005), and
98 of 5T stems by 0.2% (95% CI = -0.2%, 0.7%; P = 0.27). Stems exceeding the critical height
99 thresholds were 1.6-5.1 times more prevalent in the 5T sample than in the random sample (Fig.
100 3D).

101 Another reason 5T sampling estimated a faster rate of height increase compared to
102 random sampling was that 5T stems responded more strongly to reduced herbivory than did
103 random stems. This was evident from a linear mixed model of log-transformed stem height fitted
104 to data pooled across the two sampling methods. A model with an interaction between dummy
105 variables for browsing and sampling method outperformed a similar model with only main
106 effects (χ_1^2= 106.69, P < 0.001). The interaction indicated that the absence of browsing increased
107 height of 5T stems by 33% [95% CI = (29%, 36%), P < 0.001] and of random stems by 14%

108 [95% CI = (13%, 16%), $P < 0.001$; Fig. 3E). Correlations between annual point estimates of
109 average browse probability (Fig. 3A) and stem height (Fig. 3B) likewise indicated that the
110 inverse relationship between herbivory and stem height was stronger for 5T stems ($R^2 = 0.92$)
111 than it was for random stems ($R^2 = 0.34$; Fig. 3F). The tallest stems may have grown taller in the
112 absence of herbivory because they occurred where growing conditions were especially favorable
113 (abundant light, adequate moisture, and more basic soils[27,28]). Additionally, because tall stems
114 were browsed less (Fig. 3C), they may have also allocated relatively fewer resources to defense
115 chemistry expression[29], which would have further accelerated height growth[30].

116 If we define the cascading effect of wolves on young aspen as the annual percentage of
117 stands with mean stem height exceeding the reach of elk[15,16,18,20], 5T sampling combined with a
118 lenient assumption about browse escape height (>200 cm) estimated an effect 3-44 times greater
119 than that estimated by random sampling with a similar or stricter assumption about browse
120 escape height (>300 cm; Fig. 4). Browse probability of stems >200 cm was as high as 0.44 (95%
121 CI = 0.38, 0.51) for 5T stems and 0.32 (95% CI = 0.24, 0.41) for random stems, whereas browse
122 probability of all stems >300 cm was nearly zero (≤ 0.05; Fig. 3C).

123 Although 5T sampling grossly overestimated the average increase in aspen regeneration
124 following wolf reintroduction, it correctly showed that an increase was underway. Nevertheless,
125 even the more modest increase shown by random sampling cannot be attributed to wolves alone.
126 This is because wolves were not the sole cause of the elk population decline[10,31], and there is
127 scant evidence that they frightened elk away from aspen or any other habitat[32,33]. A weak
128 cascading effect of wolves is consistent with theory that predicts little or no such effect in food
129 webs like northern Yellowstone that feature resource limitation, reticulation (trophic levels with
130 multiple species with similar resource requirements), and environmental heterogeneity (*4*).

Understanding how predators shape large terrestrial ecosystems is a challenge made urgent by the rapid pace of global environmental change, including the extirpation and recovery of large carnivorous land mammals[34,35]. Our results demonstrate how deviations from basic sampling principles can distort this understanding. Nonrandom sampling overestimated the strength of a hypothesized trophic cascade in the system we studied, but it may underestimate cascading effects in other systems. In observational studies of large terrestrial ecosystems that lack control, randomization is an essential guard against unreliable inferences and the misguided policy and management decisions they may spawn. Fidelity to principled sampling is also vital to address growing concern about the reliability of many scientific findings[36,37].

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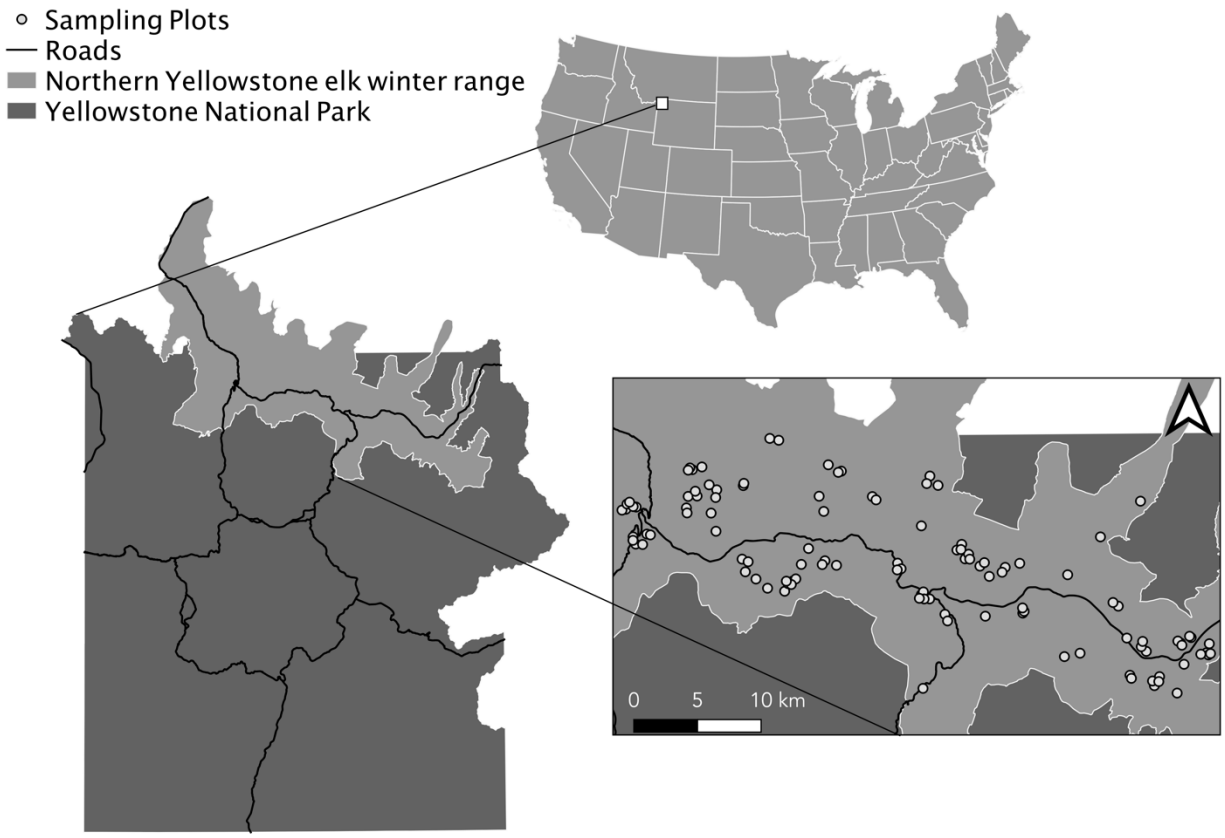

Fig. 1. Location of sampled aspen stands. The northern Yellowstone elk winter range is the maximum distribution of the northern Yellowstone elk population during winter when elk often browse young aspen.

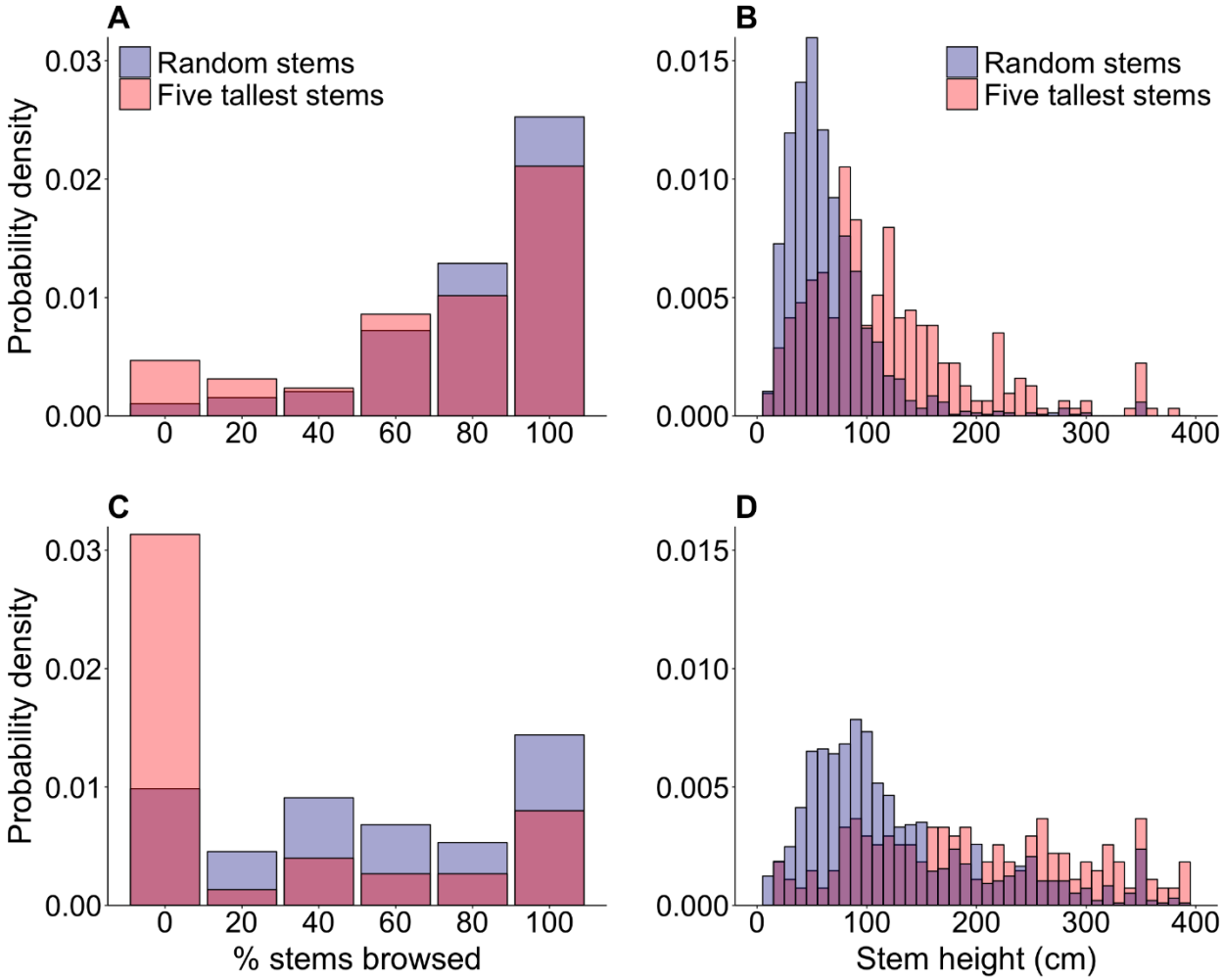

Fig. 2. Selective sampling of the five tallest young aspen describe distributions of herbivory levels and stems heights that differ from distributions estimated by random sampling. Low herbivory levels (**A** and **C**) and tall heights (**B** and **D**) were more characteristic of the five tallest young aspen throughout the study from 2007 (**A** and **B**) to 2017 (**C** and **D**).

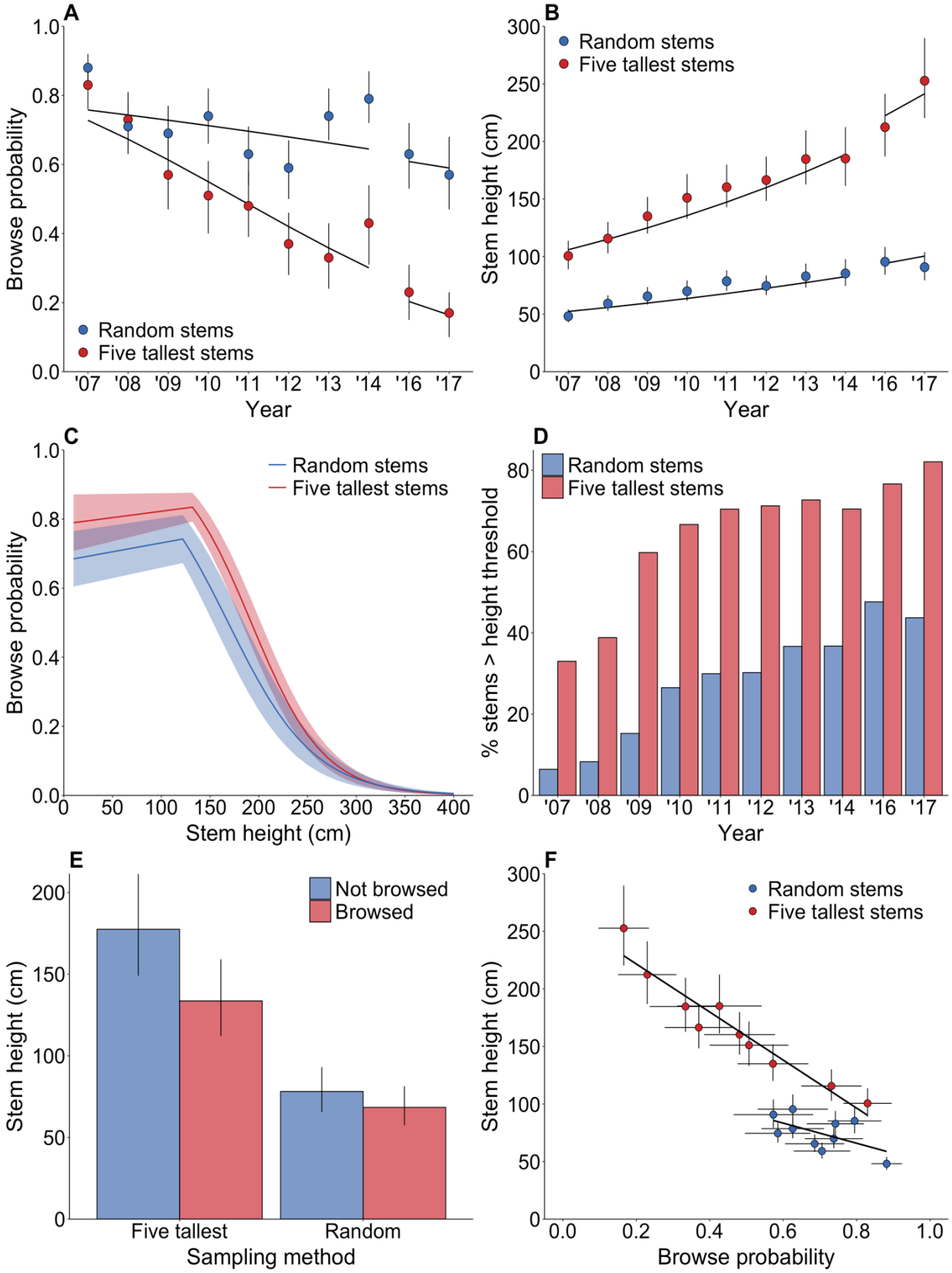
A
Browse probability
Random stems
Five tallest stems
Year
B
Stem height (cm)
Random stems
Five tallest stems
Year
C
Browse probability
Random stems
Five tallest stems
Stem height (cm)
D
% stems > height threshold
Random stems
Five tallest stems
Year
E
Stem height (cm)
Not browsed
Browsed
Five tallest
Random
Sampling method
F
Stem height (cm)
Random stems
Five tallest stems
Browse probability

Fig 3. Effects of nonrandom sampling on estimates of herbivory and height of young aspen. (**A**) Relative to a random sample, a nonrandom sample of the five tallest stems estimated a faster decrease in herbivory, and a (**B**) faster increase in stem height that were explained by how (**C**) stems exceeding critical height thresholds beyond which herbivory decreased were (**D**) more prevalent in the nonrandom sample (N=317-518 per year) than in the random sample (N=1027-1748 per year), and by how (**E** and **F**) stems in the nonrandom sample responded more strongly to reduced herbivory than did those in the random sample. Results in (A)-(C) and (E)-(F) are population-averaged fitted values with 95% confidence intervals from best-fit models.

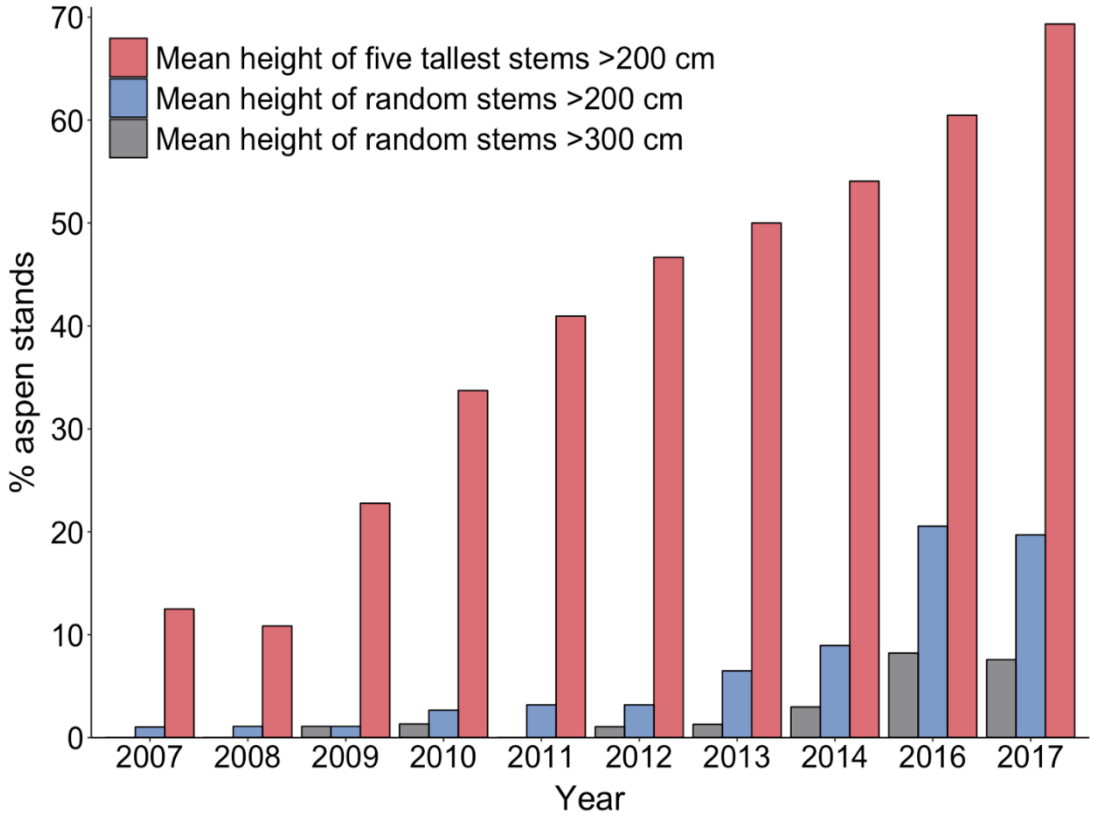

Fig. 4. Effect of nonrandom sampling on estimates of regeneration of overstory aspen stems. Bars indicate the annual percentage of sampled aspen stands in which the mean height of the five tallest stems and randomly sampled stems exceeded a presumed browse-escape height of 200-cm or 300-cm. No stands had a mean height of random stems >300-cm in 2007, 2008, and 2011.

231

Methods

Study area

We measured aspen within the portion of the northern Yellowstone elk winter range that lies within Yellowstone National Park (Fig. 1). This 995-km^2 area is defined by the low-elevation (2000-2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries near the Park's northern border. Sagebrush steppe (mainly big sagebrush [*Artemisia tridentata*]), Idaho fescue [*Festuca idahoensis*], and blue-bunch wheatgrass [*Pseudoroegneria spicata*]) is the dominant plant community at lower elevations, with conifer forests (mainly Douglas fir [*Pseudotsuga menziesii*] and lodgepole pine [*Pinus contorta*]) at higher elevations. Aspen (*Populus tremuloides*) are scattered in discrete stands on relatively moist mid-elevation benches, near streams, and along conifer forest/shrub steppe ecotones[38].

Low elevations in the study area create the warmest and driest conditions in the Park, providing important winter range for ungulates, including elk (*Cervus canadensis*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). Elk have been the most abundant ungulate species in the study area for most of the time since Park establishment in 1872[38], reaching an estimated 17,740 individuals during winter 1994-1995[39]. Subsequent decreases in elk numbers and increases in bison numbers led bison to overtake elk as the most numerous ungulate in the study area beginning winter 2011-2012. From winter 1995-1996 to winter 2014-2015, elk numbers decreased from 15,913 to 1,853, whereas bison numbers increased from 681 to 2,164. During this same period, estimated numbers of elk in the winter range outside the Park varied between 2,449 and 5,147, and annually exceeded those inside the Park beginning winter 2011-2012[39]. Approximate numbers of elk and bison

254 wintering in the study area during each year of our study (2007-2017) ranged from 1,200-6,000
255 elk and 1,400-3,200 bison.
256 Wolves were reintroduced to Yellowstone National Park in 1995-1997[40] and their annual
257 distribution has been concentrated in the study area[41]. Other large carnivores in the study area
258 included cougar (*Puma concolor*), brown bear (*Ursus arctos*), and black bear (*Ursus*
259 *americanus*). All four predators preyed on elk, with bears killing mainly calves[42], and cougars
260 and wolves killing calves and adults[43,44]. Elk that moved beyond the study area into adjacent
261 areas of Montana were also subject to predation from human hunters regulated by Montana Fish,
262 Wildlife, and Parks[45]. Humans were the only significant predator of bison, and this included
263 management removals at the Park boundary, as well as regulated hunting in adjacent areas of
264 Montana[46].
265
266 **Study population**
267 Aspen is the most widely distributed native tree species in North America and one of the few
268 upland deciduous tree species in Yellowstone National Park. It is a clonal species that mainly
269 regenerates by root sprouting with occasional seedling establishment after fire and other
270 disturbances. Root sprouting produces genetically identical trees from a common root system
271 that may be substantially older than the age of the oldest tree, which is rarely more than 150
272 years. Aspen requires moist soils and occurs mostly in areas with at least 38 cm of annual
273 precipitation[47]; the study area is near this lower limit[48]. Although aspen is a minor cover type in
274 the arid portions of its range, it is a major source of biological diversity, providing habitat for
275 numerous plants and animals[49,50]. Various ungulate species, for example, eat the leaders and
276 twigs of young aspen stems, especially during winter**.** Persistent herbivory of a stem's leader

277 prevents its growth to tree height, a process that has contributed to loss of overstory aspen in
278 parts of western North America, including the study area[51,52].

279 Historic landscape photographs suggest that overstory aspen covered approximately 4-
280 6% of the study area during 1880-1900[38,53]. Aerial photographs indicate that aspen coverage
281 decreased to 2-3% in the 1970s [38] and to as little as 1% in the 1990s[54]. Poor regeneration of tree-
282 sized aspen was noted in the study area as early as the 1920s and attributed to herbivory from
283 beaver[55] and elk[56,57]. As beaver abundance declined[58] and elk abundance remained high[38],
284 subsequent observers emphasized the role of elk herbivory in preventing aspen regeneration,
285 with some considering it a proximal factor, secondary to fire suppression and climate
286 variation[38,59,60], and others judging it an ultimate factor[51,61,62]. Romme et al.[63] concluded that the
287 dearth of aspen regeneration was not the work of any single factor, but involved the combined
288 action of multiple factors including fire suppression, drying climate, and high levels of elk
289 herbivory possibly linked to the extirpation of wolves.

290 Studies conducted in advance of wolf reintroduction did not predict any cascading effects
291 of wolves on aspen or other plant species[59]. Nevertheless, subsequent research proposed that
292 regeneration of tree-sized aspen is a necessary function of wolves reducing elk herbivory[64,65].
293 Consistent with this hypothesis, the first evidence of substantial numbers of unprotected aspen
294 reaching tree height since the early- to mid-20th century[7,48] occurred about a decade after wolf
295 reintroduction[11]. Although this pattern favors future increases in overstory aspen, climate
296 warming is expected to reduce suitable habitat for aspen in the study area within the next 40-80
297 years[66].

298

299 **Data collection**

300 We measured herbivory and height of young aspen in 113 plots distributed randomly across the
301 study area (Fig. 1). Each plot was a 1 m × 20 m belt transect set randomly within an aspen stand
302 that was itself randomly selected from an inventory of aspen stands. The inventory was a list of
303 992 landscape grid cells (240 m × 360 m) across the study area that contained at least one aspen
304 stand. A "stand" was a group of tree-size aspen in which each tree was ≤ 30 m from every other
305 tree. Aspen stands were identified from 83 color infrared aerial photographs (1:24,000) taken in
306 October 1988. To identify stands, a 1.0 cm × 1.5 cm grid of 96 cells (240 m × 360 m ground
307 dimensions) was overlain on each photograph, and a scanning stereoscope was used to identify
308 all cells containing at least one aspen stand. In these aerial photographs, aspen were identifiable
309 as white crowns, whereas conifers appeared as red crowns [48]. One hundred and thirteen grid cells
310 were randomly selected from the inventory (11% of 992 cells), one aspen stand was randomly
311 selected from each cell, and one plot was established in each stand, with the start point and
312 transect direction randomly determined [26].
313 We measured aspen at the end of the growing season from late July to September,
314 focusing on plants that were ≤ 600 cm tall, which we term "young aspen". For each aspen stand,
315 we measured every young aspen rooted within a *plot* ('random stems'), as well as each of the
316 five tallest young aspen rooted within the *stand* ('5T stems'). For each type of young aspen, we
317 measured herbivory (browsed or unbrowsed) and height of the leader stem (the tallest stem). A
318 leader was considered 'browsed' if its growth from the previous growing season had been eaten.
319
320 **Statistics**
321 First, we examined frequency distributions of herbivory levels and heights of random stems and
322 5T stems for the first and last years of the study (2007, 2017) to visualize the extent that

323 characteristics of the tallest young aspen represented those of the general population. To do so, we
324 calculated probability densities of herbivory levels and stem heights using kernel density
325 estimation with a Gaussian distribution scaled to integrate to one. Separate probability densities
326 were calculated for random stems and 5T stems for each year. Individual stands and plots were the
327 units of analysis in the probability densities of herbivory, with stands pertaining to 5T stems and
328 plots pertaining to random stems. Herbivory of 5T stems equaled the percentage of the five tallest
329 stems within a stand that were browsed, providing one of six possible values: 0%, 20%, 40%, 60%,
330 80%, and 100%. Herbivory of random stems was the percentage of young stems within a plot that
331 were browsed, and we rounded these values to the nearest of the preceding percentages to enable
332 comparison with 5T stems (Fig. 2, A and C; 2007: N_{5T} = 64 stands, N_{Random} = 97 plots; 2017: N_{5T}
333 = 75 stands, N_{Random} = 66 plots). Sample sizes were less than 113 in these data because some
334 stands/plots were not sampled or contained no young stems. The individual stem was the unit of
335 analysis in the probability densities of height, with individual heights pooled across stands and
336 plots for each year (Fig. 2, B and D; 2007: N_{random} = 369, N_{5T} = 315; 2017: N_{random} = 1027, N_{5T} =
337 1540).

338 Second, we used mixed-effects models to analyze how selective sampling of 5T stems
339 influenced estimates of annual changes in herbivory (stem-level probability of browsing) and
340 stem height. To do so, we combined measurements of 5T stems and random stems into a single
341 dataset of all stems (N = 18,623) across all years (N = 10 years; 2007-2014, 2016-2017), and
342 tested how the effect of year on herbivory and height of individual stems differed by sampling
343 method. Specifically, we treated the individual stem as the unit of analysis and tested for an
344 interactive effect of year and sampling method on (a) whether a stem was browsed, and (b)
345 height of the stem. Year was an integer that ranged from 1 (2007) to 11 (2017), and sampling

346 method was a dummy variable (1 = 5T sampling; 0 = random sampling). We analyzed models
347 with year specified as a continuous or categorical variable.

348 Models included a random intercept for stand identity and a random slope for year, which
349 permitted stand-specific trends in herbivory and stem height. The random intercept also
350 controlled for correlation among measurements of the same stand in multiple years and
351 unmeasured stand-related effects including soil, water, and light conditions. We used logistic
352 regression to analyze the probability a stem was browsed (1 = browsed; 0 = not browsed), and
353 linear regression to analyze stem height (cm). We log-transformed stem heights prior to analysis
354 to ensure that model residuals approximated a normal distribution. Fitted values from models of
355 stem height were back-transformed to the linear scale to facilitate interpretation.

356 To test how 5T sampling affected estimates of annual changes in herbivory and stem
357 height, we used likelihood ratio tests to compare models with and without a year × sampling
358 method interaction. Models including this interaction outperformed those that did not regardless
359 of whether the effect of year was treated as continuous (herbivory: χ_1^2= 134.60, $P < 0.001$;
360 height: χ_1^2= 49.42, $P < 0.001$) or categorical (herbivory: χ_9^2= 170.03, $P < 0.001$; height: χ_9^2=
361 144.12, $P < 0.001$). We calculated population-averaged fitted values of herbivory (Fig. 3A) and
362 stem height (Fig. 3B) from the interaction models by deriving marginal expectations of the
363 responses averaged over the random effects but conditional on the observed variables. We used
364 models including the continuous year × sampling method interaction to calculate and compare
365 annual changes estimated via 5T sampling and random sampling. Annual decrease in herbivory
366 equaled one minus the odds ratio for the effect of year on the probability of browsing,
367 conditional on the sampling method. Annual increase in stem height equaled $\left[\left(e^{\beta}\right) - 1\right] \times 100$

368 where β was the coefficient estimate for the continuous effect of year on stem height conditional
369 on sampling method.

370 Third, we quantified the influence of stem height on browse probability to identify the
371 height at which stems escaped herbivory. Using mixed-effects logistic regression models, we
372 analyzed stem heights on a linear scale and estimated separate models for 5T stems (N = 4,265)
373 and random stems (N = 14,358). Models specified stand identity and year as crossed random
374 intercepts, such that the random intercept for stand *i* was shared across all years for a given stand
375 *i*, whereas the random intercept for year *j* was shared by all stands in a given year *j*. This random
376 effects structure accounted for correlation between measurements taken on the same stand in
377 multiple years and on multiple stands in the same year. It also accounted for unmeasured stand-
378 and year-related effects.

379 We used piecewise linear splines to identify the threshold stem height beyond which the
380 probability of browsing decreased. To determine the presence and position of height-specific
381 thresholds, we evaluated separate sets of competing models for 5T and random stems. Each
382 model set included models with a single knot placed from 10-200 cm at 1 cm or 10 cm intervals,
383 a model with no knot representing the hypothesis of no threshold in browsing, and an intercept-
384 only model representing the null hypothesis that stem height had no effect on browsing
385 (Extended Data Tables 2, 3). A knot was the join point between two linear splines. We selected
386 knots *a priori* based on the standard assumption that aspen stems taller than 200 cm escape
387 herbivory and join the overstory[61]. Our placement of knots was consistent with guidelines for the
388 efficient use of knots[67,68]. By definition, knots selected *a priori* are fixed (i.e., not random
389 variables) and are therefore not estimated as parameters in models. We constructed variables

390 containing a linear spline for stem height so that the estimated coefficients measure the slopes of
391 the segments before and after a given knot.

392 We evaluated competing models using information-theoretic statistics[69]. Our scope of
393 inference concerned the population, so we performed model selection using marginal
394 likelihoods. The most parsimonious model was the one with the lowest Akaike Information
395 Criterion (adjusted for small sample, AIC_c) and smallest ΔAIC_c. ΔAIC_c equals the AIC_c for the
396 model of interest minus the smallest AIC_c for the set of models being considered. The best model
397 has a ΔAIC_c of zero, and models with $\Delta AIC_c < 2$ are plausibly the best. To assess uncertainty
398 about the best model, we identified models with $\Delta AIC_c < 2$ as the confidence set of models
399 (analogous to a confidence interval for a mean estimate[69]; Extended Data Tables 2, 3). We used
400 odds ratios from the best models to estimate how the probability of browsing changed with
401 increasing stem height, and calculated population-averaged fitted values from these models (Fig.
402 3C) as described above. We also calculated the proportion of stems in each annual sample of 5T
403 and random stems that exceeded the height thresholds identified in the best models (Fig. 3D).

404 Fourth, we analyzed how selective sampling of 5T stems influenced estimates of the
405 effect of herbivory on stem height. Recall that a strong negative effect of herbivory on stem
406 height is considered critical evidence of a wolf-elk-aspen trophic cascade because it
407 demonstrates the mechanism connecting the lower two trophic levels[17,19]. This analysis had two
408 parts. First, we used the combined dataset of all stems to test how the effect of herbivory on
409 height of individual stems differed by sampling method. Specifically, we tested for an interactive
410 effect of herbivory (1 = browsed; 0 = not browsed) and sampling method on log-transformed
411 stem height using mixed-effects linear regression models. We specified stand identity and year as
412 crossed random intercepts, used likelihood ratio tests to compare models with and without an

herbivory × sampling method interaction, computed population-averaged fitted values from the model including the herbivory × sampling method interaction (Fig. 3E), and used this model to calculate differences in the effect of herbivory on stem height between 5T stems and random stems. Second, we examined how the relationship between annual estimates of average stem height and browse probability differed between 5T stems and random stems (Fig. 3E). These annual estimates were the fitted values of mixed-effect models of herbivory and stem height that specified year as a categorical variable (Fig. 3, A and B). We used simple linear regression to compute the coefficient of determination for each relationship.

Finally, we assessed how selective sampling of 5T stems together with different assumptions about browse escape height influenced estimates of regeneration of overstory aspen stems. Following previous studies[15,16,18,20], we measured regeneration of overstory stems as the percentage of sampled aspen stands that showed evidence of stems taller than the presumed reach of elk. Specifically, we measured the annual percentage of sampled aspen stands in which the mean height of 5T stems and randomly sampled stems exceeded a presumed browse-escape height of 200-cm or 300-cm (Fig. 4).

Data Availability: Data are archived in Dryad (##).

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Additional Information:

Extended Data is available for this paper.

Supplementary Information is available for this paper.

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515 **Extended Data**

516 **Extended Data Table 1.** Refereed articles showing annual trends in height and (or) herbivory of
517 young aspen in Yellowstone National Park attributed to the cascading effects of wolves. Number
518 of the article cited in the main text (Ref.), number of the relevant data figure in the cited article
519 (Fig.), source of data shown in relevant data figure (Data Source), timespan covered by the data
520 (Data Years), type of data collected (Height, Herbivory), and method of data collection (selective
521 sampling of the five tallest young aspen [Five Tallest] or random sampling of all young aspen
522 [Random]) are given for each article. Checkmarks indicate which data were collected and with
523 which sampling method. Shaded cells indicate articles that reproduced data originating from
524 Ripple and Beschta (2007), and dashed-outlined cells indicate articles that reproduced data
525 originating from Painter et al. (2014). Underlined data in Peterson et al. (2014) were unpublished
526 data from E. Larsen, some of which were the subject of the current analysis.

					Data Type		Sampling Method	
Authors (Year)	Ref.	Fig.	Data Source	Data Years	Height	Herbivory	Five Tallest	Random
Ripple & Beschta (2007)	*11*	1c-d	Original data (98 stands)	1998-2006	✓	✓	✓	
Beschta & Ripple (2009)	*13*	8b	Ripple & Beschta (2007)	1999-2005	✓	✓	✓	
Ripple & Beschta (2012)	*14*	1c-d	Ripple & Bestchta (2007) Original data (resampled 98 stands)	1998-2006 2010	✓	✓	✓	
Beschta & Ripple (2016)	*17*	3g	Ripple & Bestchta (2007, 2012)	1998-2006, 2010	✓		✓	
Beschta et al. (2018)	*19*	2b-c	Ripple & Bestchta (2007, 2012) Original data (60 additional stands)	1999-2006, 2010 2005-2015	✓	✓	✓	

Extended Data Table 1 continued

Authors (Year)	Ref.	Fig.	Data Source	Data Years	Data Type		Sampling Method	
					Height	Herbivory	Five Tallest	Random
Painter et al. (2014)[1]	*15*	7a	Original data (87 stands)	2003-2012	✓	✓	✓	
Peterson et al. (2014)	*10*	1c	Painter et al. (2014) Original data (113 stands)	2003-2012 1999-2013[2]	✓		✓	✓
Painter et al. (2015)[1]	*16*	2a	Painter et al. (2014)	2003-2012	✓		✓	
Beschta et al. (2016)	*18*	5c	Painter et al. (2014)	2002[3]-2012		✓	✓	
Painter et al. (2018)[1]	*20*	3a	Ripple & Bestchta (2007, 2012) Painter et al. (2014)	1999-2006, 2010 2005-2012		✓	✓	
Halofsky et al. (2008)[4]	*12*	3a-b	Original data (44 stands)	1995-2004	✓	✓	✓	

[1] Included data from a random sample of young aspen in Yellowstone National Park that provided no information on annual trends in height, and little or no information on annual trends in herbivory. The latter was limited to changes in herbivory during 1997-1998 and 2011-2012 reported in Painter et al. (2014, 2015).

[2] No data for 2000 and 2003

[3] Source of 2002 data was not specified.

[4] Sampled the three tallest young aspen within a stand.

534 **Extended Data Table 2.** Model selection results for GLMMs describing the effect of stem
535 height (ht) on the probability that a "five tallest" young aspen was browsed in northern
536 Yellowstone National Park. Variables ht1 and ht2 contain a linear spline at the indicated knot
537 (cm). The intercept and simple linear models included no knot. All models included random
538 effects for stand identity and year. Log-likelihood (LL), number of parameters (*K*), AIC_c,
539 differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (*W*) are
540 given for each model. The best model ($\Delta AIC_c = 0.00$) is in boldface and competitive models
541 ($\Delta AIC_c < 2.00$) are shaded.

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*W*
intercept	-	-2166.41	3	4339.04	749.59	0.00
ht	-	-1845.00	4	3698.36	108.92	0.00
ht1, ht2	10	-1845.00	5	3700.55	111.11	0.00
ht1, ht2	20	-1839.17	5	3688.90	99.46	0.00
ht1, ht2	30	-1830.38	5	3671.32	81.87	0.00
ht1, ht2	40	-1822.30	5	3655.16	65.72	0.00
ht1, ht2	50	-1817.03	5	3644.62	55.17	0.00
ht1, ht2	60	-1813.72	5	3638.01	48.56	0.00
ht1, ht2	70	-1810.72	5	3632.01	42.57	0.00
ht1, ht2	80	-1808.52	5	3627.60	38.16	0.00
ht1, ht2	90	-1802.95	5	3616.47	27.03	0.00
ht1, ht2	100	-1797.70	5	3605.96	16.52	0.00
ht1, ht2	110	-1793.95	5	3598.46	9.01	0.00
ht1, ht2	111	-1793.71	5	3597.98	8.54	0.00
ht1, ht2	112	-1793.46	5	3597.48	8.04	0.00
ht1, ht2	113	-1793.19	5	3596.94	7.49	0.00
ht1, ht2	114	-1792.95	5	3596.47	7.03	0.00
ht1, ht2	115	-1792.75	5	3596.07	6.62	0.00

Extended Data Table 2 continued

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*W*
ht1, ht2	116	-1792.61	5	3595.78	6.34	0.00
ht1, ht2	117	-1792.47	5	3595.51	6.07	0.00
ht1, ht2	118	-1792.36	5	3595.27	5.83	0.00
ht1, ht2	119	-1792.17	5	3594.91	5.47	0.01
ht1, ht2	120	-1792.02	5	3594.59	5.15	0.01
ht1, ht2	121	-1791.77	5	3594.11	4.67	0.01
ht1, ht2	122	-1791.53	5	3593.62	4.18	0.01
ht1, ht2	123	-1791.28	5	3593.12	3.67	0.01
ht1, ht2	124	-1791.06	5	3592.68	3.24	0.02
ht1, ht2	125	-1790.89	5	3592.33	2.89	0.02
ht1, ht2	126	-1790.57	5	3591.69	2.25	0.03
ht1, ht2	127	-1790.27	5	3591.10	1.66	0.03
ht1, ht2	128	-1789.96	5	3590.49	1.04	0.05
ht1, ht2	129	-1789.70	5	3589.97	0.52	0.06
ht1, ht2	130	-1789.53	5	3589.63	0.18	0.07
ht1, ht2	131	-1789.47	5	3589.51	0.06	0.07
ht1, ht2	**132**	**-1789.44**	**5**	**3589.44**	**0.00**	**0.08**
ht1, ht2	133	-1789.48	5	3589.51	0.07	0.07
ht1, ht2	134	-1789.52	5	3589.61	0.16	0.07
ht1, ht2	135	-1789.61	5	3589.77	0.33	0.07
ht1, ht2	136	-1789.65	5	3589.86	0.41	0.06
ht1, ht2	137	-1789.75	5	3590.06	0.61	0.06
ht1, ht2	138	-1789.89	5	3590.35	0.90	0.05
ht1, ht2	139	-1790.07	5	3590.71	1.26	0.04
ht1, ht2	140	-1790.33	5	3591.23	1.79	0.03
ht1, ht2	141	-1790.66	5	3591.88	2.44	0.02
ht1, ht2	142	-1791.00	5	3592.56	3.11	0.02

Extended Data Table 2 continued 542

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*W*
ht1, ht2	143	-1791.37	5	3593.31	3.86	0.01
ht1, ht2	144	-1791.85	5	3594.25	4.81	0.01
ht1, ht2	145	-1792.34	5	3595.23	5.79	0.00
ht1, ht2	146	-1792.80	5	3596.15	6.71	0.00
ht1, ht2	147	-1793.25	5	3597.06	7.62	0.00
ht1, ht2	148	-1793.70	5	3597.97	8.53	0.00
ht1, ht2	149	-1794.21	5	3598.98	9.54	0.00
ht1, ht2	150	-1794.70	5	3599.97	10.53	0.00
ht1, ht2	160	-1799.25	5	3609.06	19.62	0.00
ht1, ht2	170	-1803.13	5	3616.83	27.39	0.00
ht1, ht2	180	-1807.42	5	3625.39	35.95	0.00
ht1, ht2	190	-1811.10	5	3632.77	43.33	0.00
ht1, ht2	200	-1813.79	5	3638.13	48.69	0.00

543 **Extended Data Table 3.** Model selection results for GLMMs describing the effect of stem
544 height (ht) on the probability that a randomly sampled young aspen was browsed in northern
545 Yellowstone National Park. Variables ht1 and ht2 contain a linear spline at the indicated knot
546 (cm). The intercept and simple linear models included no knot. All models included random
547 effects for stand identity and year. Log-likelihood (LL), number of parameters (*K*), AIC_c,
548 differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (*W*) are
549 given for each model. The best model ($\Delta AIC_c = 0.00$) is in boldface and competitive models
550 ($\Delta AIC_c < 2.00$) are shaded.

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*W*
intercept	-	-8238.90	3	16484.05	1028.55	0.00
ht	-	-7886.08	4	15780.57	325.08	0.00
ht1, ht2	10	-7885.74	5	15782.08	326.59	0.00
ht1, ht2	20	-7886.00	5	15782.60	327.11	0.00
ht1, ht2	30	-7883.24	5	15777.08	321.58	0.00
ht1, ht2	40	-7877.04	5	15764.69	309.20	0.00
ht1, ht2	50	-7859.22	5	15729.05	273.56	0.00
ht1, ht2	60	-7835.44	5	15681.48	225.99	0.00
ht1, ht2	70	-7803.77	5	15618.14	162.65	0.00
ht1, ht2	80	-7776.04	5	15562.69	107.19	0.00
ht1, ht2	90	-7755.96	5	15522.53	67.04	0.00
ht1, ht2	100	-7738.23	5	15487.07	31.58	0.00
ht1, ht2	110	-7726.73	5	15464.07	8.58	0.00
ht1, ht2	111	-7726.10	5	15462.81	7.32	0.00
ht1, ht2	112	-7725.49	5	15461.59	6.10	0.00
ht1, ht2	113	-7724.91	5	15460.43	4.94	0.01
ht1, ht2	114	-7724.41	5	15459.43	3.94	0.01
ht1, ht2	115	-7724.08	5	15458.78	3.28	0.02

Extended Data Table 3 continued

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*W*
ht1, ht2	116	-7723.73	5	15458.07	2.58	0.03
ht1, ht2	117	-7723.49	5	15457.58	2.08	0.03
ht1, ht2	118	-7723.15	5	15456.91	1.42	0.05
ht1, ht2	119	-7722.91	5	15456.43	0.94	0.06
ht1, ht2	120	-7722.62	5	15455.85	0.35	0.08
ht1, ht2	121	-7722.51	5	15455.63	0.14	0.09
ht1, ht2	**122**	**-7722.44**	**5**	**15455.49**	**0.00**	**0.09**
ht1, ht2	123	-7722.47	5	15455.54	0.05	0.09
ht1, ht2	124	-7722.55	5	15455.70	0.20	0.08
ht1, ht2	125	-7722.68	5	15455.97	0.47	0.07
ht1, ht2	126	-7722.81	5	15456.22	0.73	0.06
ht1, ht2	127	-7722.99	5	15456.58	1.09	0.05
ht1, ht2	128	-7723.19	5	15456.98	1.49	0.04
ht1, ht2	129	-7723.39	5	15457.39	1.90	0.04
ht1, ht2	130	-7723.66	5	15457.92	2.42	0.03
ht1, ht2	131	-7723.99	5	15458.60	3.10	0.02
ht1, ht2	132	-7724.36	5	15459.33	3.84	0.01
ht1, ht2	133	-7724.81	5	15460.24	4.74	0.01
ht1, ht2	134	-7725.26	5	15461.12	5.63	0.01
ht1, ht2	135	-7725.81	5	15462.22	6.72	0.00
ht1, ht2	136	-7726.37	5	15463.35	7.86	0.00
ht1, ht2	137	-7727.03	5	15464.66	9.17	0.00
ht1, ht2	138	-7727.75	5	15466.11	10.62	0.00
ht1, ht2	139	-7728.53	5	15467.68	12.18	0.00
ht1, ht2	140	-7729.36	5	15469.33	13.84	0.00
ht1, ht2	141	-7730.18	5	15470.96	15.47	0.00
ht1, ht2	142	-7731.08	5	15472.76	17.27	0.00

Extended Data Table 3 continued

Model	Knot (cm)	LL	*K*	AIC_c	ΔAIC_c	*w*
ht1, ht2	143	-7732.01	5	15474.64	19.14	0.00
ht1, ht2	144	-7733.11	5	15476.82	21.33	0.00
ht1, ht2	145	-7734.31	5	15479.23	23.74	0.00
ht1, ht2	146	-7735.54	5	15481.68	26.19	0.00
ht1, ht2	147	-7736.72	5	15484.05	28.56	0.00
ht1, ht2	148	-7737.86	5	15486.32	30.83	0.00
ht1, ht2	149	-7739.02	5	15488.64	33.15	0.00
ht1, ht2	150	-7740.22	5	15491.05	35.56	0.00
ht1, ht2	160	-7749.68	5	15509.98	54.48	0.00
ht1, ht2	170	-7760.17	5	15530.95	75.46	0.00
ht1, ht2	180	-7771.68	5	15553.96	98.47	0.00
ht1, ht2	190	-7781.88	5	15574.36	118.86	0.00
ht1, ht2	200	-7793.35	5	15597.31	141.82	0.00