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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Population density of North American elk: effects on plant diversity

Kelley M. Stewart · R. Terry Bowyer · John G. Kie · Brian L. Dick · Roger W. Ruess

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Abstract Large, herbivorous mammals have profound effects on ecosystem structure and function and often act as keystone species in ecosystems they inhabit. Density-dependent processes associated with population structure of large mammals may interact with ecosystem functioning to increase or decrease biodiversity, depending on the relationship of herbivore populations relative to the carrying capacity (*K*) of the ecosystem. We tested for indirect effects of population density of large herbivores on plant species richness and diversity in a montane ecosystem, where increased net aboveground primary productivity (NAPP) in response to low levels of herbivory has been reported. We documented a positive, linear relationship between plant-species diversity and richness with NAPP. Structural equation modeling revealed significant indirect relationships between population density of herbivores, NAPP, and species diversity. We observed an indirect effect of density-dependent processes in large, herbivorous mammals and species diversity of plants through changes in NAPP in this montane ecosystem. Changes in species diversity of plants in response to herbivory may be more indirect in ecosystems with long histories of herbivory. Those subtle or indirect effects of herbivory may have strong effects on ecosystem functioning, but may be overlooked in plant communities that are relatively resilient to herbivory.

Keywords North American elk · Herbivore optimization · NAPP · Species diversity · Species richness · Structural equation models

Introduction

Large herbivores often act as keystone species (sensu Molvar et al. 1993; Simberloff 1998) in ecosystems they inhabit, and may either increase or decrease plant diversity, depending on their population density relative to the carrying capacity (*K*) of the ecosystem. Large mammals have unique population dynamics, they exhibit strong density-dependent population growth (McCullough 1979; Stewart et al. 2005), and unique life-history characteristics; those species are not simply small mammals scaled large (Caughley and Krebs 1983). Dynamics and density-dependent processes associated with populations of large mammals may have cascading effects on ecosystem function and community structure, including changing levels of biodiversity (Person et al. 2001; see Bowyer et al. 2005 for review). DeCalesta and Stout (1997) reported that interactions between populations of large mammals and their environments should be standardized to *K* to provide understanding of effects of large mammals on

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K. M. Stewart (✉)
Natural Resources and Environmental Science,
University of Nevada Reno, 1000 Valley Rd/MS 186,
Reno, NV 89512, USA
e-mail: kstewart@cabnr.unr.edu

R. T. Bowyer · J. G. Kie
Department of Biological Sciences, Idaho State University,
921 South 8th Avenue, Stop 8007, Pocatello, ID 83209, USA

B. L. Dick
United States Forest Service, Pacific Northwest Research
Station, 1401 Gekeler Lane, La Grande, OR 97850, USA

R. W. Ruess
Institute of Arctic Biology and Department of Biology and
Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775,
USA

their environments. High-levels of herbivory, from populations of large herbivores at or near *K*, often lead to declines in plant species diversity and loss of highly palatable species from the plant community (Olff and Ritchie 1998; Rooney 2001; Vellend 2004; McShea 2005; Nicholson et al. 2006). Indeed, loss of plant diversity may have cascading effects on other trophic levels in the ecosystem (Berger et al. 2001; Terborgh et al. 2001). Conversely, herbivory by large mammals at low to moderate densities has led to positive influences on ecosystem functioning, such as increasing net aboveground primary productivity (NAPP) and increased nutrient cycling with inputs of urine and feces—a process known as herbivore optimization (McNaughton 1979; Ruess and McNaughton 1987; Ruess et al. 1989; Hik and Jefferies 1990; Frank and McNaughton 1993; Stewart et al. 2006). Thus, plant responses to herbivory depend on the intensity of foraging, which is determined by population density of herbivores relative to carrying capacity (*K*) of the ecosystem (Kie et al. 2003; Persson et al. 2005; Stewart et al. 2006). We define low to moderate levels of herbivory as population density of herbivores that is at or below the maximum number of recruits (e.g., maximum sustained yield—MSY) for a population with density-dependent growth (McCullough 1979; Fowler 1981).

Species composition is likely a major determinant of stability, primary productivity, nutrient dynamics, invasibility, and other critical attributes of ecosystems (Tilman 1999). Low levels of herbivory may upset competitive interactions among plants and prevent particular species from dominating a community (Pastor and Cohen 1997; Jacobs and Naiman 2008). Thus, at low levels, grazing or browsing reduces biomass and canopy cover, primarily of competitively dominant plants, which leads to increases in spatial heterogeneity, and in turn allows more species of plants to coexist (Olff and Ritchie 1998; Jacobs and Naiman 2008). Conversely, high levels of herbivory often led to declines in plant species richness and diversity, as plant species are reduced or eliminated by herbivory or by trampling, and generally those species that are resistant to herbivory or trampling are more likely to remain in the ecosystem (Olff and Ritchie 1998; Vellend 2004; McShea 2005; Nicholson et al. 2006; Jacobs and Naiman 2008). Finally, communities that are more diverse often are more productive and resistant to disturbance, including effects from herbivory (Tilman 1999; Collins et al. 1998). Vegetation plots with high species diversity in Serengeti grasslands were more resistant to grazing and had higher productivity than less-diverse plots (McNaughton 1983, 1985).

North American elk (*Cervus elaphus*) are an especially good model for examining effects of herbivores at high and low density in montane ecosystems. Life-history characteristics of elk are consistent with species that exhibit strong density dependence; elk populations show reductions in physical condition and pregnancy rates at high population density (Stewart et al. 2005). These large mammals occur extensively across the intermountain west of North America and consume a variety of forages, thereby affecting species richness and diversity of most functional groups of plants (Kie et al. 2003; Stewart et al. 2003). Stewart et al. (2006), in a companion study to this paper, reported herbivore optimization by North American elk in this same montane ecosystem, and observed increases in NAPP at low levels of herbivory in forbs, graminoids, and shrubs. Herbivory by elk has also been implicated both in increasing and decreasing rates of nutrient cycling in soils (Singer and Schoenecker 2003; Schoenecker et al. 2004).

Although Stewart et al. (2006) documented herbivore optimization, those authors observed no direct link between levels of herbivory and species diversity of the plant community. Our objective was to further investigate the relationship between population densities of North American elk with changes in the plant community, and to examine indirect effects of herbivory by elk on species composition of plants. The relationship between herbivore population dynamics and species composition is potentially more subtle than directly changing the species composition of the ecosystem, particularly in ecosystems with a long history of herbivory by native and domestic ungulates. Thus, herbivory may change species diversity of plants indirectly by changing the productivity of those plants. We hypothesize that those indirect effects of herbivores on species composition at low population densities of herbivores modify plant communities more strongly than selective removal of palatable species. Furthermore, we hypothesize that the relationship between species composition of the plant community and herbivory is mediated through changes in NAPP with varying levels of herbivory. Based on those hypotheses, we predict that, in areas of low herbivory by elk where NAPP has been documented (Stewart et al. 2006) to be increased compared with areas of no or high herbivory (e.g. the hump of the herbivore optimization curve), we will observe increased species richness and diversity of plants.

Materials and methods

Study area

We conducted research from 1999 through 2001 on the Starkey Experimental Forest and Range (hereafter Starkey) of the U.S. Forest Service. Starkey (45°13′N, 118°31′W) is situated in the Blue Mountains of northeastern Oregon, USA, and is located 35 km southwest of La Grande, Oregon. Elevations on Starkey range from 1,120 to 1,500 m. Starkey encompasses 10,125 ha, and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores, including migration to traditional winter ranges (Rowland et al. 1997; Stewart et al. 2002, 2006).

We restricted our experiment to the northeast area on Starkey (Fig. 1), which encompassed 1,452 ha, and was separated from the remainder of the study area by the same high fence (Stewart et al. 2002). The northeast area was divided into 2 study sites with the 2.4-m fence, east (842 ha) and west (610 ha), to accommodate experimental comparisons of two population densities of elk (Fig. 1). We divided the northeast area in a manner that resulted in plant communities being equal in proportions in eastern and western areas (Stewart et al. 2002). Such study sites are sufficiently large to allow natural movements and other behaviors of large herbivores (Hirth 1977; McCullough 1979; Stewart et al. 2002). Stewart et al. (2002) examined locations of elk in the northeast study area and reported no significant effects of the high fence on habitat selection by elk.

Elk no longer migrate off the study area to traditional winter ranges because of the fence; consequently, animals were maintained throughout winter in a holding area and were fed only a maintenance diet of alfalfa hay (Rowland et al. 1997; Stewart et al. 2005, 2006). Elk were held on the winter feedground from early December until late April (Rowland et al. 1997; Stewart et al. 2006). Few elk remained on the study area during winter; thus, herbivory by elk in our study was restricted to spring, summer, and autumn (Stewart et al. 2002, 2005, 2006). Because of the design of the Starkey Project, the elk population can be manipulated nonlethally by releasing specific numbers of animals into each study area via a system of fenced alleyways between the feedground and each of the study areas on Starkey (Main Study, Campbell, Northeast east, Northeast west; Stewart et al. 2005, 2006).

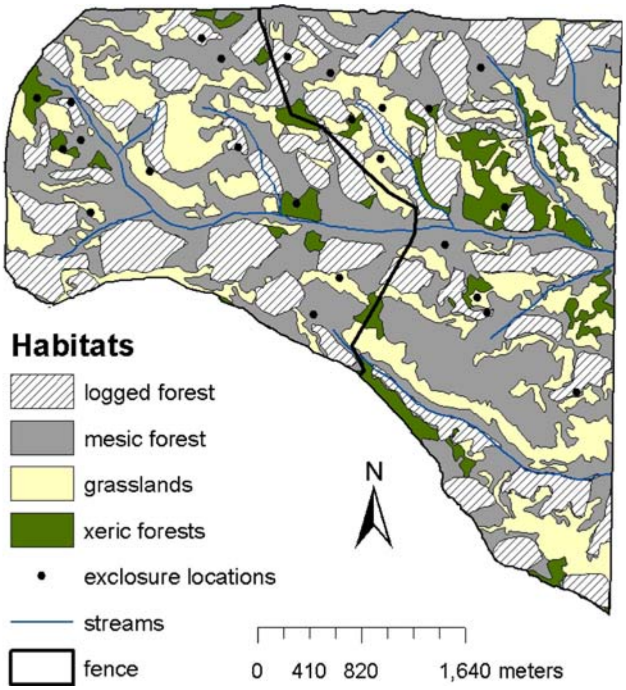

Fig. 1 The northeast study area with low density (west 4.1/km^2) and high density (east 20.1 elk/km^2) of North American elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, Oregon, USA. Four major plant communities are indicated with locations of herbivore exclosures

Data were collected on physical condition, body mass, and pregnancy rates of female elk as they entered the winter feedground each year (Rowland et al. 1997; Stewart et al. 2002, 2005). Summer is the time of resource acquisition for ungulates in seasonal environments (Mautz 1978), and elk in this study were documented to show density-dependent reductions in physical condition and pregnancy rates, based on resource acquisition during summer (Stewart et al. 2005). Those results indicate that density dependence is driving population dynamics in this ecosystem, regardless of elk spending the winter on our feedground rather than traditional winter ranges (Stewart et al. 2005).

The northeast area consisted of 4 major plant communities: (1) mesic forest, (2) xeric forest, (3) xeric grassland, and (4) logged forest (Stewart et al. 2002: Fig. 3). Plant nomenclature follows Hitchcock and Cronquist (1996). Mesic forests occur on north-facing slopes with overstory composition dominated by grand fir (*Abies grandis*). Xeric forests generally occur on south- and east-facing slopes; tree composition consisted primarily of Ponderosa pine (*Pinus ponderosa*), with the understory dominated by elk sedge (*Carex geyeri*; Stewart et al. 2002). Xeric grasslands occur primarily on south- and east-facing slopes; this plant community was dominated by a few grasses such as Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Agropyron spicatum*), and forbs such as low gumweed (*Grindelia nana*; Stewart et al. 2002). Logged-forest communities composed areas where timber was harvested during 1991–1992. Grand fir on Starkey suffered widespread mortality (>90%) from spruce budworm (*Choristoneura occidentalis*) during the late 1980s, and timber was harvested in areas where most trees were killed (Rowland et al. 1997; Stewart et al. 2002). Following removal of trees, those areas were seeded with several species of grasses including orchardgrass (*Dactylis glomerata*), and bluegrass (*Poa* spp.; Stewart et al. 2002).

Experimental design and statistical analyses

During 1997, we initiated an experiment to examine effects of population density of elk on net aboveground plant productivity and offtake of plant biomass by those large herbivores. We created two populations of elk at high and low density relative to *K*, in the northeast east and west study areas on Starkey (Fig. 1). We assessed vegetation responses to herbivory by examining elk populations maintained at high population density near carrying capacity (*K*) based on physical condition of elk on Starkey, which we estimated to be 20.1 elk/km^2; and at low densities near or below maximum sustained yield (MSY), which we estimated at 4.1 elk/km^2 (Stewart et al. 2006). The high-density population was randomly assigned to the northeast east study area and the low-density population to the northeast west study area (designation of study areas is provided in the description of the study areas). This manipulation of population density of elk began in 1998, which was a pretreatment year, and we stocked each study area with moderate densities of elk (Stewart et al. 2006). The experimental manipulation of high and low population density began in 1999, but because of a mishap that year, a gate was left open between study areas, elk densities were moderately high (10.8 elk/km^2) and low (6.6 elk/km^2; Stewart et al. 2006). Finally in 2000 and 2001, we restricted access to our study areas and we maintained our targeted high (20.1 elk/km^2) and low (4.1 elk/km^2) densities of elk (Stewart et al. 2006). Our analyses of species composition of plants include 1999–2001, when exclosures were present in all plant communities, except 6 grassland sites. Thus, NAPP in grasslands during 1999 only was restricted to areas with herbivory by elk, but grassland exclosures were established for 2000 and 2001. Stewart et al. (2006) provide a detailed rationale for this experimental design.

We placed exclosures (32 × 32 m) in mesic, logged, and xeric forests, with 3 replications per community for each high and low-density treatment. Exclosures placed in xeric grasslands were 12 × 12 m to accommodate plant communities that occurred in smaller patches (Fig. 1). Stewart et al. (2006) used ten 1-m^2 movable exclosures located outside permanent exclosures in mesic, logged, and xeric forests and five movable exclosures in xeric grasslands (McNaughton 1979; McNaughton et al. 1996). We clipped 0.25-m^2 quadrates inside and outside movable exclosures once a month during spring and summer to assess productivity of vegetation (Stewart et al. 2006). We sampled permanent exclosures with 0.25-m^2 quadrates at the beginning and end of each season to examine NAPP in the absence of herbivory and to compare with areas grazed by elk (Stewart et al. 2006). We used those estimates of NAPP in the presence and absence of herbivores for our comparisons with species diversity and richness of plants. Because we were interested in the range of NAPP with measures of species composition across the study area, habitats were combined for those analyses. Our replications consisted of permanent exclosure locations (inside and outside), 3 exclosures in each of 4 plant communities per treatment (high and low population density), for a total of 24 sampling sites. We understand that these sites are replicated within our 2 density treatments (e.g., 12 sampling sites in each density treatment). Large herbivores, including elk, do not use habitat uniformly, each of our study areas is greater than 600 ha, and population density and use of each of those sampling locations likely is independent of the others.

We determined species composition of plants using step-point transects inside and outside each permanent exclosure (Bowyer and Bleich 1984; Bleich et al. 1997; Stewart et al. 2006). We recorded a cover “hit” if the point (<1 mm in diameter) fell within the canopy of a shrub or on a stem or leaf of a plant. Each transect contained approximately 200 step-points outside the exclosure and 100 step-points inside the exclosure, primarily because of limited space within exclosures (Stewart et al. 2006). Adequate sample size was determined by plotting the number of species against cumulative number of points sampled (Kershaw 1964; Geysel and Lyon 1980; Stewart et al. 2006). We used the Shannon-Weiner formula (H') to estimate species diversity of plants from step-points for cover inside and outside each exclosure (Ricklefs 1999; Krebs 1999; Zar 1999).

Ungulates do not use habitat uniformly (Fretwell 1972; Fryxell 1991; Kie et al. 2003) and some exclosure locations in the high density area received less herbivory than some locations in the low density area (Stewart et al. 2006). Thus, the treatment density of elk for each study area was inappropriate for estimating grazing intensity at each exclosure (Stewart et al. 2006). Accordingly, we used population densities of elk calculated outside each exclosure for each year determined by Stewart et al. (2006). Those densities were determined using radio telemetry locations of elk, calculating density maps by using those locations, which were then smoothed using kriging for each year (Stewart et al. 2006). Eight adult females and four adult males per year were equipped with radio collars in each study area; error rate on telemetry locations was <50 m (Stewart et al. 2002, 2006). Estimates of density at each exclosure site were used to infer grazing intensity at each sampling location outside each exclosure (Stewart et al. 2006). Stewart et al. (2006) provides detailed description of methods used to estimate those densities. Mean densities at exclosures in each of the study areas are provided in Table 1.

We used linear regression to compare species richness and diversity of plants with NAPP across our study areas (Zar 1999). We also used linear regression to compare plant species diversity with NAPP, both in the presence and absence (exclosures only) of herbivory (Zar 1999). We fit structural equation models (Grace 2006) for effects of elk population density on plant species richness and diversity (Fig. 4a). Structural equation models attempt to describe the multivariate patterns between traits conditional on a

Table 1 Descriptive statistics (mean ± SD) for plant variables for no herbivory (inside exclosures) by North American elk (*Cervus elaphus*), and mean densities of herbivores in the low (4.1 elk/km^2) and high (20.1 elk/km^2) density study areas

Variable	No herbivory ($n = 72$)	Low herbivory ($n = 36$)	High herbivory ($n = 36$)
Population density (elk/km^2)[a]	0	5.0 ± 2.22	16.0 ± 6.32
NAPP (g m^{-2} day^{-1})[a]	0.60 ± 0.884	1.65 ± 1.855	1.27 ± 1.758
Plant species richness	17.0 ± 6.74	19.8 ± 6.88	20.0 ± 7.10
Plant species diversity (H')	13.1 ± 5.43	13.3 ± 5.11	13.9 ± 5.03

Population densities of herbivores were determined at each sampling site from animal locations to estimate levels of herbivory, on the Starkey Experimental Forest and Range 1999–2001, Oregon, USA

[a] From Stewart et al. (2006)

specific ordering of structural relationships that are inferred from explicit biological hypotheses (Vile et al. 2006). Thus, this method is appropriate for examining direct effects of population density of elk on NAPP and indirect effects of elk on species composition of plants (Vile et al. 2006; Bellingham and Sparrow 2009). We fit data to the conceptual model as structural equation models using AMOS student version 5.0.1. software (SPSS, Illinois, USA).

Results

We observed significant relationships between NAPP and species richness ($r^2 = 0.042$, CV = 36.91, $F_{1,136} = 5.91$, $P < 0.001$) and diversity ($r^2 = 0.054$, $CV = 38.07$, $F_{1,136} = 7.76$, $P < 0.001$) across study areas. Those regressions, however, had relatively low fit, based on low r^2 values, and low predictability based on low values for coefficients of variation (Fig. 2). Population density of elk did not affect species diversity directly (Table 1). We observed no relationship between NAPP and species diversity, in areas without herbivory (e.g., inside exclosures; $F_{1,64} = 0.81$, $P = 0.373$). Although in areas with herbivory by elk (e.g., outside exclosures), the relationship between NAPP and species diversity was highly significant ($r^2 = 0.095$, $CV = 35.44$, $F_{1,70} = 7.33$, $P = 0.008$; Fig. 3); although again those regressions had relatively low predictability and fit.

Structured equation models indicated significant quadratic relationships between population density and NAPP ($P = 0.007$), and a positive relationship with diversity and NAPP ($P = 0.005$; Fig. 4b). Structured equation models performed well and indicated a significant, indirect relationship between population density and species richness

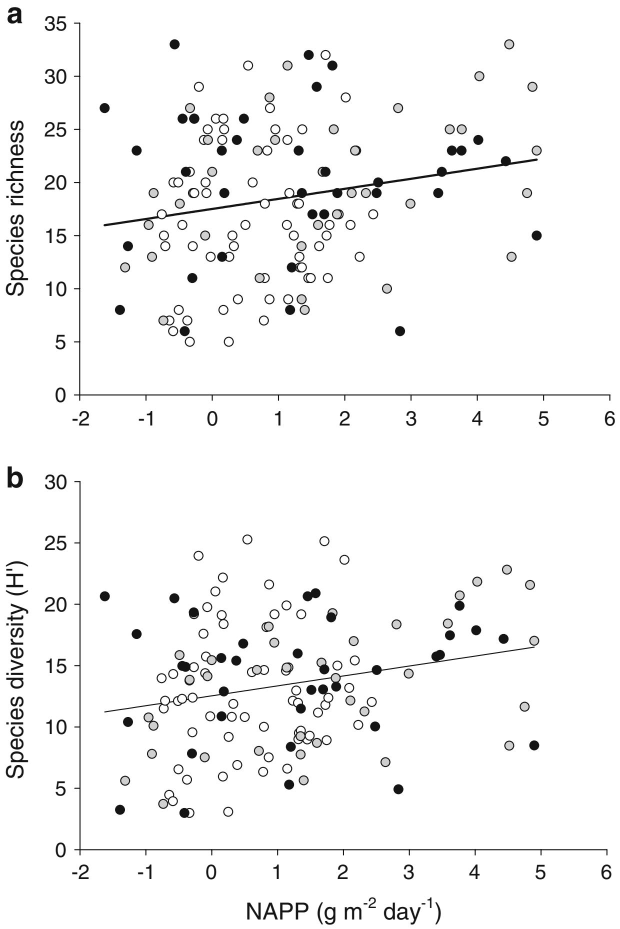

Fig. 2 Relationship between net aboveground primary production (*NAPP*) with **a** plant species richness and **b** plant species diversity on the Starkey Experimental Forest, La Grande, Oregon, USA, 1999–2001. *White circles* indicate sampling locations in areas without herbivory, *gray circles* are locations near exclosures in the study area with low-density of elk, and *black circles* are locations near exclosures in the study area with high-density of elk. *Linear regression* indicated a positive relationship between NAPP and species richness (**a**) ($\hat{Y} = 17.51 + 0.95x$, $r^2 = 0.042$, $F_{1,136} = 5.91$, $P = 0.016$) and NAPP and species diversity (**b**) ($\hat{Y} = 12.54 + 0.81x$, $r^2 = 0.054$, $F_{1,136} = 7.76$, $P = 0.006$)

and diversity of plants (Fig. 4b). R^2 values for these models were relatively low, indicating low predictability. We observed significant paths between population density (and population density^2) with NAPP ($P = 0.007$), then NAPP with species diversity ($P = 0.005$), which indicated a significant indirect effect of herbivory by elk on species diversity of plants (Fig. 4b).

Discussion

Our research hypotheses were supported—in the areas where NAPP was increased, we also observed increased species richness and diversity of plants. Our data indicate

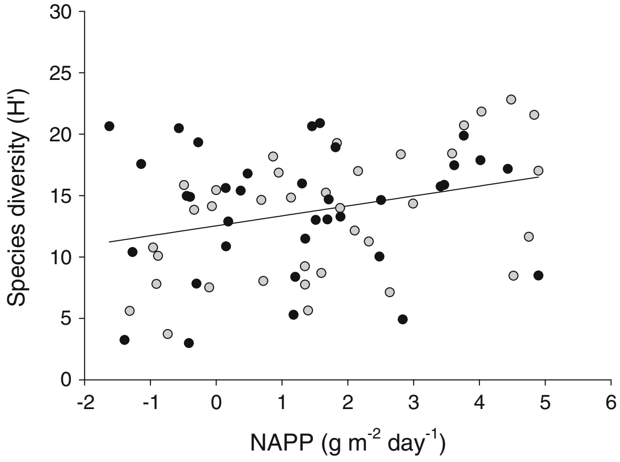

Fig. 3 Relationship between net aboveground primary production (*NAPP*) and plant species diversity in the presence of herbivory by North American elk (outside exclosures only); linear regression also indicated a positive relationship between NAPP and species diversity of plants ($\hat{Y} = 12.38 + 0.86x$, $F_{1,70} = 7.33$, $r^2 = 0.095$, $P = 0.008$) on the Starkey Experimental Forest, La Grande, OR, USA 1999–2001. *Gray circles* are locations near exclosures in the study area with low-density of elk, and *black circles* are locations near exclosures in the study area with high-density of elk

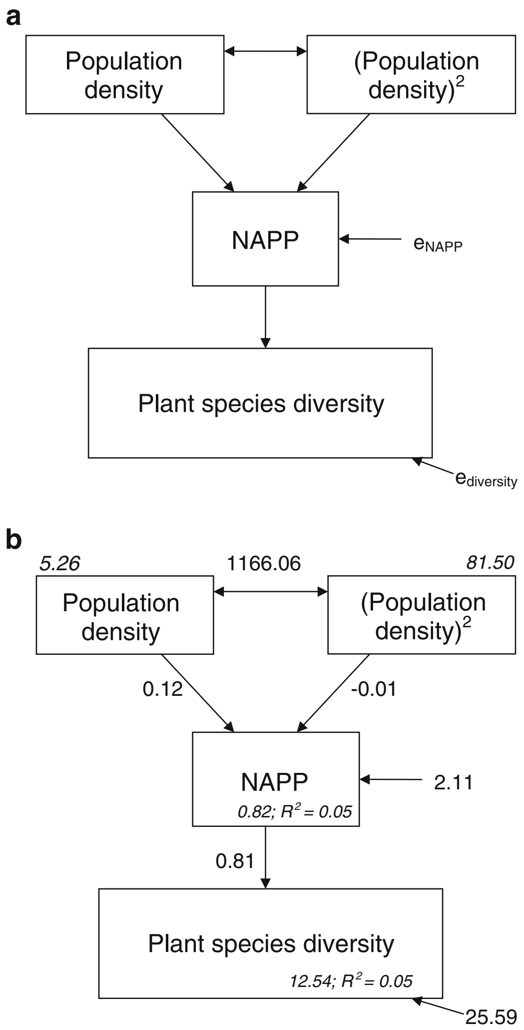

Fig. 4 Structural equation model testing hypothesized relationships for effects of population density of North American elk on net aboveground primary production (NAPP) and species diversity of plants. **a** Hypothetical structural equation model. *One-headed arrows* represent causal relationships, and *double-ended arrows* indicate correlation between variables (e.g., population density and population density squared). Residual error variables (e_i) represent effects of unexplained causes (Vile et al. 2006). **b** Structural equation model derived from model a. Path coefficients between variables are unstandardized partial regression coefficients. *Arrows* not originating from a variable represent residual error variances. Intercept values are provided in *italics* next to *boxes* with variable names. Response *boxes* contain the intercept and R^2 value in *italics*. *Arrows* indicate significant ($P < 0.005$) paths between variables. Overall goodness-of-fit $X^2_2 = 6.155$; $P = 0.05$

an indirect effect of population density of a large herbivore on species composition through changing levels of NAPP; low to moderate levels of herbivory had the greatest NAPP, species richness, and species diversity in this montane ecosystem. Regressions of NAPP and species diversity inside exclosures without herbivory by elk were not significant, although the relationship between NAPP and species diversity was significant in areas with herbivory by elk. Ungulates do not use habitat uniformly and herbivory outside exclosure locations varied greatly within density treatments (Fretwell 1972; Fryxell 1991; Kie et al. 2003). Indeed, in some instances, exclosure locations in the high-density area received levels of herbivory similar to or occasionally lower than locations in the low-density treatment. Thus increases in NAPP with low levels of herbivory occurred at locations in both low and high density treatments (Figs. 2, 3). Simply comparing NAPP and species richness or diversity by study area and treatment density (e.g., no herbivory, high density, and low density) was too coarse an examination to detect the fine-scale effects of herbivory by elk on the plant community that we observed in this study.

When we investigated indirect effects of population density on species diversity using structured equation models, our hypothesis was supported; we observed significant relationships of population density on NAPP and through NAPP on species diversity. Results of those two regressions and the structured equation model suggest that herbivory may be driving the relationship between NAPP and species diversity. In areas with herbivory by elk, the relationship between NAPP and species diversity, although significant, had relatively low predictability, most likely because of great variation in NAPP across the differing plant communities on the study area. We were unable to determine, however, if increases in NAPP directly increase diversity or if the effects of herbivores on interactions among plants lead to both increases in NAPP and species diversity. Further investigation to determine the mechanism driving those relationships among herbivores, NAPP, and species diversity is warranted.

Stewart et al. (2006) suggested that where plants have a long history of grazing and browsing, changes in species composition with changing levels of herbivory may not be evident. Indeed, Starkey has been grazed by both native and domestic ruminants since the turn of the century (Skovlin 1991). Since Starkey was fenced in 1987, cattle were grazed in the northeast study area at moderate density by researchers from Oregon State University. Although cattle were removed from our study area prior to 1997 when we began our experiment, effects of long-term herbivory from domestic ruminants likely remain, such that most of the species present in our study areas probably are resilient to herbivory (Cingolani et al. 2005; Stewart et al. 2006). Communities that are more resilient to herbivory may be more likely to respond to changes in densities of herbivores indirectly through changes in NAPP rather than rapidly changing species composition (Cingolani et al. 2005; Stewart et al. 2006). This process is likely to be overlooked if the community is resilient to herbivory and indirect responses are not examined.

We do not imply that large herbivores do not affect species diversity directly; at high levels of herbivory, palatable species of plants have been shown to be negatively affected in both eastern deciduous and western coniferous forests, or those plants may be removed completely (Rooney and Gross 2003; Rooney and Waller 2003; Beschta and Ripple 2008). Indeed, high densities of herbivores, exhibiting density-dependent feedbacks on measures of fitness (Gaillard et al. 2000), can drive successional changes leading to dominance of plant species of lower nutritional value, slower rates of nutrient cycling (Pastor and Cohen 1997; Tremblay et al. 2005; Stewart et al. 2006), and restricted regeneration of palatable shrubs and trees such as black cottonwood (*Populus trichocarpa*) and bigleaf maple (*Acer macrophyllum*; Beschta and Ripple 2008). Indeed, trophic cascades resulting from high densities of herbivores following removal of carnivores has been observed in multiple ecosystems (Terborgh et al. 2001; Ripple and Beschta 2004; Beschta and Ripple 2008). Mulder and Ruess (1998) demonstrated that the herbivory by brant geese (*Branta bernicla nigricans*) altered the competitive environment among plants in a subarctic salt marsh community, and changed biomass allocation and sexual reproduction in grazed plants. Moreover, high population densities of geese (*Anser* sp.) resulting from agricultural subsidies on winter ranges have resulted in conversion of summer range in the Canadian arctic from coastal salt marshes to mudflats (Jefferies 2000; Jefferies and Rockwell 2002; Fox et al. 2005). At a local scale, those geese have begun to show density-dependent feedbacks resulting from lowered carrying capacity on the summer range. Indeed, reduced growth and survival of young indicate that those populations are rapidly approaching carrying capacity (Person et al. 2003; Abraham et al. 2005; Fox et al. 2005).

Ungulates act as keystone species in many ecosystems that they inhabit, and at high population density those populations have been observed to have negative effects on nutrient cycling, plant productivity, and species composition (Augustine and McNaughton 1998; Rooney 2001; Beschta and Ripple 2008), while simultaneously showing negative feedbacks on physical condition and reproduction associated with density dependence (Stewart et al. 2005). Indeed, changing successional patterns resulting from high levels of herbivory is not uncommon when herbivore densities are close to carrying capacity. Tremblay et al. (2005) suggested that because white-tailed deer (*Odocoileus virginianus*) switched from their primary forage balsam fir (*Abies balsamea*) to alternatives, such as lichens, which incidentally are higher quality forage than fir (Hodgman and Bowyer 1985; Ditchkoff and Servello 1998; Jenks and Leslie 1989), those populations somehow escaped density-dependent feedbacks. Nevertheless, those authors also reported that the deer population appeared to be stable over 25 years (Tremblay et al. 2005), which is a strong indicator of density-dependent feedbacks regulating the population near carrying capacity. Carrying capacity is defined as the number of animals at or near equilibrium with their food supply (Kie et al. 2003); however, that definition does not mean that plant communities are static or that primary forage types need to be in equilibrium with the herbivore population. Herbivory can act as either a stabilizing influence or an agent of disturbance depending on where population density resides relative to carrying capacity (Kie et al. 2003).

Species diversity appears to be a key factor in ecosystem stability, and greater stability of plant community was observed in ecosystems with high species diversity following perturbations (McNaughton 1977; Lepŝ et al. 1982; Frank and McNaughton 1991; Tilman 1996; Mulder et al. 2001). Tilman (1996) suggested that plots with greater species richness should have a higher probability of containing disturbance-resistance species, and that high-diversity mixtures should outperform low-diversity ones. Mulder et al. (2001) reported no relationship between species richness and biomass of bryophytes under constant conditions; however, under drought conditions, biomass increased strongly with increasing species richness. Thus, Mulder et al. (2001) concluded that positive interactions among plants may be an important mechanism linking high diversity to high productivity under stressful environmental conditions. This idea applies to herbivory as well, because low-density populations of herbivores maintain high levels of diversity in plant communities (McNaughton 1983, 1985; Tilman 1999; Collins et al. 1998; Collins and Smith 2006). Those more diverse communities likely would contain mixtures of palatable and unpalatable species of plants. Restoration of bison (*Bison bison*) to rangelands decreased herbaceous cover and biomass, but increased spatial heterogeneity and species richness as standing biomass declined (Knapp et al. 1999; Jacobs and Naiman 2008).

Keystone species have the capacity to alter communities; whether those modifications are positive or negative are driven by population densities of those species relative to carrying capacity. The relationship between different levels of herbivory and biodiversity appears to be strongly linked to density-dependent processes of herbivores, and resilience of the community to herbivory (Cingolani et al. 2005; Stewart et al. 2006). Low levels of herbivory, resulting from herbivores at low population density relative to carrying capacity, likely affect biodiversity in more subtle ways than are typically addressed, particularly if those communities are relatively resilient to herbivory.

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