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ARTICLE

Large herbivores facilitate a dominant grassland forb via multiple indirect effects

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Abstract

While large herbivores are critically important components of terrestrial ecosystems and can have pronounced top-down effects on plants, our understanding of the underlying mechanisms driving these effects remains incomplete. Large herbivores can alter plant growth, reproduction, and abundance through direct effects (predominantly consumption) and through indirect effects via altered interactions with abiotic factors and other species. We know considerably less about these indirect effects than the direct effects. Here, we integrate medium- and small-scale field experiments to investigate how a large vertebrate herbivore, cattle (*Bos taurus*), affects the aboveground biomass of a dominant forb species, *Artemisia scoparia*, via diverse direct and indirect pathways in a temperate grassland in northeast China. Although cattle consumed this forb, its biomass increased significantly in response to grazing, due to multiple indirect positive effects that outweighed the direct negative effects of consumption. Cattle preferentially consumed the competing grass *Leymus chinensis*, and altered *Artemisia* microhabitats by reducing total plant cover and litter biomass and by increasing the abundance of co-occurring ant species (e.g., *Formica* spp. and *Lasius* spp.). This led to additional indirect positive effects on *A. scoparia* likely due to (1) increased light availability in understory layers and other limiting resources (e.g., soil nutrients and moisture) caused by removal of competitors and plant litter at the soil surface and (2) the changes in resource availability (e.g., soil nutrients and moisture) associated

with ant colonies. Our results show that large herbivores can affect plant growth not only via direct consumption, but also via multiple indirect effects. Focusing on the causes and consequences of herbivore-induced indirect effects will not only help us to better understand the influence of these animals in ecological systems, but will also lead to more effective land management and conservation practices in the regions they inhabit.

KEYWORDS

competition, direct and indirect effects, facilitation, plant growth, plant–herbivore interactions, top-down effects

INTRODUCTION

Large herbivores are critically important components of terrestrial landscapes and can shape the structure and functioning of ecological systems by exerting strong top-down pressure on plants (Augustine & McNaughton, 1998; Forbes et al., 2019; Knapp et al., 1999; Milchunas et al., 1988; Wang et al., 2019). However, wild large herbivores worldwide are facing dramatic declines in diversity, distribution, and abundance due to hunting, land-use changes, and habitat fragmentation (Daskin & Pringle, 2018; Dirzo et al., 2014; Ripple et al., 2015). Likewise, many mammalian herbivores are increasingly introduced into ecosystems either as livestock (e.g., about 25 million have been added to the planet per year over the last 50 years) or naturalized alien species in habitats that lack grazing history in recent evolutionary times (Ripple et al., 2015; Vázquez & Simberloff, 2004; Wardle et al., 2001). In the face of such trends, understanding how large herbivores control the growth, abundance, and distribution of plant species is of fundamental importance, especially for developing predictions about the structure and functioning of ecological systems and implementing effective conservation and management strategies (Maclean et al., 2011; Smit et al., 2015; Young et al., 2013). However, the effects of large herbivores on plant populations can be complex, as they may involve indirect effects on other plant species, the abiotic environment and other consumer species (Augustine & McNaughton, 2004; Cushman et al., 2011; Goheen et al., 2010; Riginos & Young, 2007), and understanding of the underlying mechanisms for such effects remains incomplete.

Historically, direct effects such as consumption and trampling have been assumed to be the major pathway by which large herbivores affect plants (Augustine & McNaughton, 1998; Bakker et al., 2016; Liu, Feng, et al. 2015; Liu, Kan, et al., 2015; Olff & Ritchie, 1998). However, there is growing evidence that the indirect effects of large herbivores on plants can be equal or even

greater than direct effects in some ecosystems (Goheen et al., 2004, 2010; Maclean et al., 2011; Okullo & Moe, 2012; Pringle et al., 2011). Indirect effects occur when the effects of one species on another species are mediated by a third species or by abiotic resources (Strauss, 1991). Several mechanisms of indirect effects by large herbivores on plants have been proposed or demonstrated. First, herbivores can indirectly affect a plant species by modifying the intensity of competition with neighboring plant species (Riginos & Young, 2007; Smit et al., 2007; Veblen & Young, 2010). Second, plants may be indirectly affected when large herbivores act as “ecosystem engineers” (Jones et al., 1994, 1997) and alter microhabitat characteristics by reducing vegetation and litter cover, allowing more light to reach the understory and thus enhancing seed germination and seedling recruitment (Borer et al., 2014; Howison et al., 2015; Porensky et al., 2013). Third, large herbivore activities may affect the abundance and distribution of co-occurring animals (e.g., insect herbivores, pollinators, seed dispersers, and decomposers, Bardgett & Wardle, 2003; Cecil et al., 2019; Foster et al., 2014; Sankaran & Augustine, 2004; van Klink et al., 2015), which may in turn modify the strength of their interactions with plants (Howison et al., 2017; Maclean et al., 2011; Veen et al., 2012). Indirect effects can be difficult to observe and detect because the interacting species are often separated spatially and temporally (Ohgushi, 2005). Given this reality, most studies infer indirect effects of large herbivores from correlations between covarying factors and plant performance (Goheen et al., 2004, 2010; Maclean et al., 2011). As far as we know, no empirical studies have yet manipulated multiple factors independently to identify the mechanisms by which these indirect effects arise.

The direct and indirect effects of large herbivores will often occur simultaneously in nature, with potentially synergistic (interactive) effects on plants (Forbes et al., 2019; Pringle et al., 2011; Rooney & Waller, 2003). Their relative importance may be context dependent and determined by the characteristics of both target plants

(e.g., palatability, defense, and regrowth ability) (Belsky, 1986; Diaz et al., 2007; Karban & Baldwin, 1997; McNaughton, 1983) and the herbivores themselves (e.g., diet selections and feeding intensity; Charles et al., 2017; McNaughton, 1978; Olff & Ritchie, 1998; Young et al., 2013). Until recently, considerably less attention has been paid to the indirect effects of herbivores, and few studies have simultaneously tested the relative importance of direct and indirect effects on plants (but see Hamilton & Frank, 2001, Goheen et al., 2010, Frank et al., 2018). Quantifying both direct and indirect effects in the same system through multiple experiments will advance our understanding of the role that herbivores play in affecting individual plants, plant populations, and communities.

In a temperate grassland in northeast China, we explored the degree to which a vertebrate herbivore, cattle (*Bos taurus*), affects the biomass and density of a dominant forb species (*Artemisia scoparia*) via multiple direct and indirect pathways. Cattle occasionally feed on *A. scoparia* but prefer the dominant grass *Leymus chinensis* (Zhu et al., 2019). Together with other grass species, *L. chinensis* annually produces a great deal of plant litter that accumulates on the soil surface and inhibits the germination and growth of *A. scoparia* and thus reduces its biomass in the early spring (from April to June) (Liu et al., 2018). Cattle grazing dramatically reduces litter cover, which allows more light to reach the soil surface, favoring ants (Li et al., 2018). The increases in ant abundance further benefit the total biomass of the whole plant community, possibly by enhancing soil nutrients and water availability (Farji-Brener & Werenkraut, 2017; Zhong et al., 2021). Hence, for this system, besides the known direct herbivore effects, we explore through additional experiments three potential indirect pathways that large herbivores may have on plants: (1) reduction of interspecific competition by suppression of *L. chinensis*; (2) modification of the physical habitat by removing the physical barriers of plant litter on the soil surface; and (3) grazing-induced increases in ant abundance (Li et al., 2018), which may enhance soil nutrients and moisture and in turn benefit plant growth of *A. scoparia* (see Zhong et al., 2021 for similar positive effects of ants on *L. chinensis*). While the direct effects of tissue removal by herbivory can be either negative or neutral, all three of these indirect pathways should exert positive impacts on *A. scoparia* biomass (see more information in Appendix S1: Figure S1). Hence, we hypothesized that cattle would have an overall neutral or even positive effect on *A. scoparia* biomass because multiple grazing-induced indirect positive effects offset, or even overcome, the negative direct effects of consumption on plants. To test this hypothesis, we explored the overall effects of cattle grazing on *A. scoparia* biomass with a medium-scale grazing experiment and used a set of small-scale experiments to

tease apart multiple direct and indirect mechanisms by which cattle affect *A. scoparia* biomass.

METHODS

Study system and background

Our study site is a semiarid (~350 m above sea level) grassland located at Grassland Ecological Research Station of Northeast Normal University, Jilin Province of Northeast China (44°35.5' N, 123°30.5' E). Mean annual temperature ranges from 4.6° to 6.4°C and annual precipitation is 280–400 mm. The site is dominated by *L. chinensis*, which accounts for 60%–90% of total canopy cover and annually accumulates a thick layer (about 10–15 cm depth) of litter on the soil surface (Liu et al., 2018). The biennial or perennial forb *A. scoparia* accounts for 10%–20% of total canopy cover (Zhong et al., 2014). *Leymus chinensis* and *A. scoparia* often grow intermingled with each other and potentially compete for both above- and belowground resources. Other plant species at our study site collectively comprise ~10%–30% cover and include grasses such as *Phragmites australis* and forbs such as *Kalimeris integrifolia*.

Since the 1970s, cattle (*B. taurus*) have been increasing in the region, and grazing pressure is controlled by human practices. Cattle are generalist herbivores and feed on the forb *A. scoparia* but prefer the grass *L. chinensis* (Zhu et al., 2019). The area hosts a high density (~0.5–4 nests every 1 m²) of nests of ants, mainly *Lasius* spp. (e.g., *L. flavus*) and *Formica* spp. (e.g., *F. sanguinea* and *F. candida*), which can significantly modify soil physicochemical properties (more details in Li et al., 2018). Grasshoppers (Orthoptera, Acrididae) are the dominant herbivorous insects, but occur in low abundance (~1–2 individuals every 1 m²) in the cattle-grazed areas (Zhu et al., 2019). Grasshoppers prefer *L. chinensis* grass and one individual can consume ~2.0 g dry mass of plant leaves in its lifetime (Feng et al., 1995). Small mammals such as rodents and hares are rarely seen (all authors, personal observations). Prior to the experiments, the study area was used for low-intensity livestock grazing and mowing, but it was fenced and the grazing and mowing activities were ended in 2005 when it became a research site.

Medium-scale grazing experiment

Experimental design

A medium-scale cattle grazing experiment was initiated in June 2009, consisting of 12 50 × 50 m plots, arranged

into six plot pairs (blocks) (Appendix S1: Figure S2). The six blocks were randomly located and separated from each other by 150–300 m and the two plots within each block were separated by approximately 30 m. For the two plots within each block, we randomly assigned one to receive cattle grazing while the other was ungrazed and served as a control. Within each of our 12 plots, we established 10 randomly positioned 1×1 m permanent quadrats separated from each other by at least 5 m (Appendix S1: Figure S2). From 2010 to 2013, the grazed plots were grazed by cattle (mean \pm SE; mass 300 ± 8 kg) at light to moderate intensity, as recommended by local governments. A total of 48 mature cows were assigned to the six grazed plots, with eight cows enclosed in each plot. Grazing occurred each year from June to August during the first 2 weeks of each month, with daily grazing occurring between 06:00–08:00 and 16:00–18:00 on each of those 14 days except in weekends, creating grazing intensities that simulated local grazing habits. This resulted in less than 50% of above-ground plant biomass consumed by cattle (all authors, unpublished data).

Assessing grazing effects on plants, litter, ants, and resource availability

We assessed the effects during two summer seasons (2010–2011) of cattle grazing on plants, litter, ants, and resource availability within all plots of our enclosure experiment by comparing initial conditions (mid-August 2009) with those measured on 27 August 2011 (i.e., peak of growing season). In both years, we estimated plant biomass by clipping plants to ground level in 1×0.2 m in one random location in the 1×1 m quadrats in each plot. Clipped vegetation was sorted to *L. chinensis*, *A. scoparia*, other plant species (grouped) and litter (e.g., all the dead material on the ground), and dried for 48 h at 70°C and weighed. In the field, plant density of the two species was estimated by counting the number of stems (reproductive culms for grass species) in each quadrat, and plant height (cm) was measured on five haphazardly chosen stems of each species. For ant abundance, we visually counted the total number of ant nests within the quadrats following Li et al. (2018).

For resource availability, we measured light penetration, soil moisture, and total availability of nitrogen (N) and phosphorus (P) in the soils. Using a GLZ-C-G PAR (photosynthetically active radiation) point sensor (Top Instrument, Zhejiang, China), we measured light penetration by taking light intensity readings from three random locations above the vegetation canopy and at the

ground surface, below litter, if present. Using a handheld soil-moisture meter with a 20-cm probe (OSA-1; OUSU Electronic Technology, Hebei, China), we measured soil moisture by taking readings from three random locations within each permanent quadrat. We measured light intensity and soil moisture on August 18 and 25, 2011 under sunny conditions with minimal cloud cover. The mean value for these two dates was used in our statistical analyses. Using a 4-cm diameter soil auger, we randomly collected three replicate soil samples at a depth of 20 cm from each permanent quadrat and then pooled these subsamples. We collected soil samples once on August 27, 2011. For each soil sample, nutrients were extracted from a 10 g soil subsample with 70 mL 2 mol/L KCl. Extracts were frozen at -4°C for analysis of NH_4^+ and NO_3^- content by continuous flow analyzer (Futura; AMS-Alliance Instruments, Frépillon, France). Soil total available N concentration was the sum of NH_4^+ and NO_3^- concentrations. We used another 10-g soil subsample to measure total available P, which was extracted using acidified $\text{NH}_4\text{OAc-EDTA}$ and analyzed by the inductively coupled plasma-atomic emission spectrometer (ICP-AES; Spectroflame, Spectro Analytical Instruments, Kleve, Germany).

Small-scale experiments

Experimental design

From 2013 to 2015, we performed a series of small-scale experiments to examine the independent effects of different direct and indirect pathways of cattle grazing (direct herbivory, clipping of *L. chinensis*, litter removal, and removal of ants) on the biomass of *A. scoparia*.

The small-scale experiments were conducted at a site adjacent to the medium-scale grazing experiment. In June 2013, we randomly established eight 3×5 m blocks, with each block containing a pair of 1×1 m permanent plots for each pathway above (see experimental layout in Appendix S1: Figure S3). In August 2013, we measured the initial conditions, including plant biomass (*L. chinensis*, other grasses, *A. scoparia*, other forbs, and their combination), litter biomass, ant nest abundance, and resource availability (light availability, soil moisture, N and P availability) in the 1×1 m plots within all blocks for each pathway using the methods we have described. In August 2015, we quantified the effects of the simulated grazing manipulations after 2 years of application (2014–2015) by reassessing the same variables above.

During the growing seasons (May–September) of 2014 and 2015, the following four manipulations were randomly assigned and applied to one plot within each of

the eight blocks, while another plot was unmanipulated and served as a control (see Appendix S1: Figure S3).

Direct effects of herbivory

We simulated the direct effect of cattle herbivory on *A. scoparia* by removing 20% of the height from 20% of the *A. scoparia* individuals in each plot.

Indirect effects of competition release

We simulated the indirect effects of cattle-induced competition release on *A. scoparia* by clipping the competing neighbor *L. chinensis*. From 50% of the *L. chinensis* individuals in each plot, we removed 30% of their height. The clipped biomass was completely removed from the plot and avoided its accumulation at soil surface.

For our simulated grazing manipulations, we removed the tissue of *A. scoparia* and *L. chinensis* once per month from June to August in 2014 and 2015. The intensity of tissue removal (the amount of plant height removed and the proportion of individual plants manipulated) accurately simulated the intensity of cattle grazing on *A. scoparia* and *L. chinensis* observed in our medium-scale grazing experiment (see Appendix S1: Figure S4). After removing plant tissue with grass clippers, we immediately applied cattle saliva with a brush to the cut stems and leaves to more realistically simulate cattle herbivory (McNaughton, 1985).

Indirect effects of litter reduction (LR)

We simulated the indirect effects of cattle-induced changes in litter abundance by removal all plant litter on the soil surface in all litter-removed plots from June to August in 2014 and 2015. We removed all the plant litter in the plots during this period, because our field observations showed that cattle grazing had nearly eliminated all the plant litter at the soil surface from June to August in the medium-scale grazing experiments (Appendix S1: Figure S5). In addition, because litter removal would potentially increase the density of ant nests (Li et al., 2018), confounding the treatment effects, we applied 1 g of poison ant baits (Jingkang Ant Bait Granules, Lekang Technology, Beijing, China) within both the plant litter removal and control plots to suppress ants from June to August. The main active ingredients of the ant bait are 0.45% Tetramethrin and 0.02% Alphacypermethrin. Jingkang Ant Bait was designed to appeal specifically to ants and has been used successfully in reducing ant abundance in this system (Li et al., 2018).

Indirect effects of ant activities

We simulated the indirect effects of cattle-induced changes on ant abundance by reducing ant abundance. Because it is difficult to simulate the increased ant abundance

observed in the grazed areas while keeping other factors, such as plant litter accumulation, unchanged, we did the opposite and suppressed ant abundance to investigate their influences on *A. scoparia* growth and population size. We randomly selected one plot within each block to apply 1 g Jingkang Ant Bait Granules to suppress ants, while the other served as the control. The Jingkang Ant Bait Granules were applied once in each month from June to August. In addition to applying ant bait to suppress ant populations, we also built plastic fences around the plots to prevent ants from entering them from nests outside the treatment plot. The fences protruded about 15 cm from the soil surface and were submerged 20 cm below the soil surface. Double-faced adhesive tape was applied to the outside surface of the fence. The fences were effective at limiting the movements of ants, with workers regularly observed being trapped by the glue and unable to climb over the fences (Z. Zhong, personal observations).

Data analyses

All statistical analyses were performed using R 3.1.0 software.

Medium-scale grazing experiment

For the medium-scale grazing experiments, we averaged all response variables for the 10 quadrats in each plot and used these 10 means in the statistical analyses. We used linear mixed-effect models (lme), with grazing treatment (ungrazed or grazed) as a fixed effect and block as a random effect, to assess the impacts of 2 years (2010–2011) of cattle grazing on aboveground biomass, density, and stem height of *A. scoparia*, biomass of *L. chinensis* and litter, ant-nest density, and resources availability (light penetration, soil moisture, N and P availability). All response variables were tested for normality and homogeneity of variance and log- or square-root-transformed as needed. Because there were no significant treatment effects for the initial conditions (Appendix S1: Tables S1–S3), the analyses above were applied only to the post-treatment data. These analyses were completed using the function lme from the package nlme.

Small-scale experiments

For the small-scale experiments, we used similar linear mixed-effects models, with treatments (*A. scoparia* clipping, *L. chinensis* reduction [LCR], LR, and ant reduction

[AR]) treated as fixed effects and the block as random effects to assess the influence of 2 years (2014–2015) of each manipulated factor on the aboveground biomass of *A. scoparia*, and resources availability (light penetration, soil moisture, N and P availability). As before, all response variables were tested for normality and homogeneity of variance and transformed as needed. In addition, we again performed our analyses on to the post-treatment data because there were no significant treatment effects at the beginning of the experiments (Appendix S1: Tables S4 and S5).

We used the relative change in *A. scoparia* biomass and resource availability to quantify the strength of each pathway that cattle affect this forb and the potential mechanisms underlying these effects. We calculated relative change in *A. scoparia* biomass as (mean *A. scoparia* biomass in the treatment plots – mean *A. scoparia* biomass in the untreated plots)/(mean *A. scoparia* biomass in the treatment plots) \times 100. The relative changes in resource availability were calculated by using the same method.

RESULTS

Medium-scale grazing experiment

Effects of cattle grazing on plants, litter, ants and resource availability

Cattle increased *A. scoparia* biomass by 43% ($F_{1,5} = 10.04$, $p = 0.025$, Figure 1a) and stem density by 45% ($F_{1,5} = 27.06$, $p = 0.003$, Figure 1b) after 2 years of grazing (2010–2011). Mean height of *A. scoparia* was not significantly affected by cattle grazing ($F_{1,5} = 0.97$, $p = 0.371$, Figure 1c). Grazing reduced biomass of *L. chinensis* by 13%, but this difference was not significant ($F_{1,5} = 4.74$, $p = 0.081$, Figure 2a). However, grazing significantly reduced litter biomass by 71% ($F_{1,5} = 72.77$, $p < 0.001$, Figure 2b) and increased ant nest density by 113% ($F_{1,5} = 23.35$, $p = 0.005$, Figure 2c). Moreover, cattle grazing significantly increased understory light penetration by 207% ($F_{1,5} = 50.36$, $p = 0.001$, Figure 3a) and increased soil total available N by 37% ($F_{1,5} = 31.79$, $p = 0.003$, Figure 3c). Cattle had no significant effect on soil moisture ($F_{1,5} = 1.95$, $p = 0.224$, Figure 3b) or total available P ($F_{1,5} = 2.11$, $p = 0.216$, Figure 3d).

Small-scale experiments

Direct effects of herbivory

Simulated consumption of *A. scoparia* by cattle reduced its biomass by 4%, but this effect was not significant

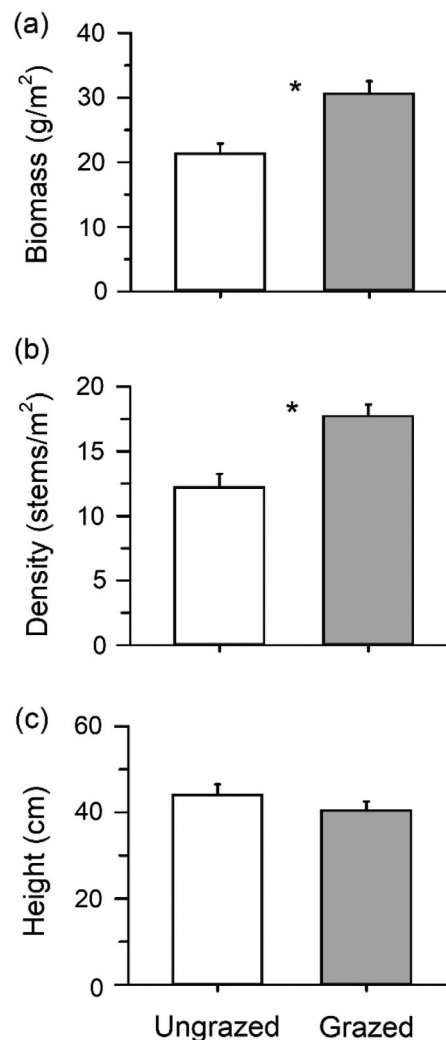


FIGURE 1 Effects of 2 years (2010–2011) of cattle grazing on (a) biomass, (b) density, and (c) height of *Artemisia scoparia* in the medium-scale grazing experiment. Asterisks indicate a significant differences (* $p < 0.05$). Error bars represent SE

($F_{1,7} = 1.49$, $p = 0.262$, Figures 4a and 5a). Simulated consumption did also not significantly affect soil moisture, N or P availability (Table 1).

Indirect effects of competition release

Clipping *L. chinensis* increased *A. scoparia* biomass by 24% ($F_{1,7} = 17.44$, $p = 0.004$, Figures 4b and 5a). LCR increased the light penetration to the soil surface by 85% ($F_{1,7} = 75.74$, $p < 0.001$, Table 1, Figure 5b), whereas it did not significantly affect soil moisture, or N or P availability (Table 1).

Indirect effects of plant litter

Litter removal significantly increased *A. scoparia* biomass by 40% ($F_{1,7} = 13.07$, $p = 0.009$; Figures 4c and 5a), increased light penetration to the soil surface by 74%

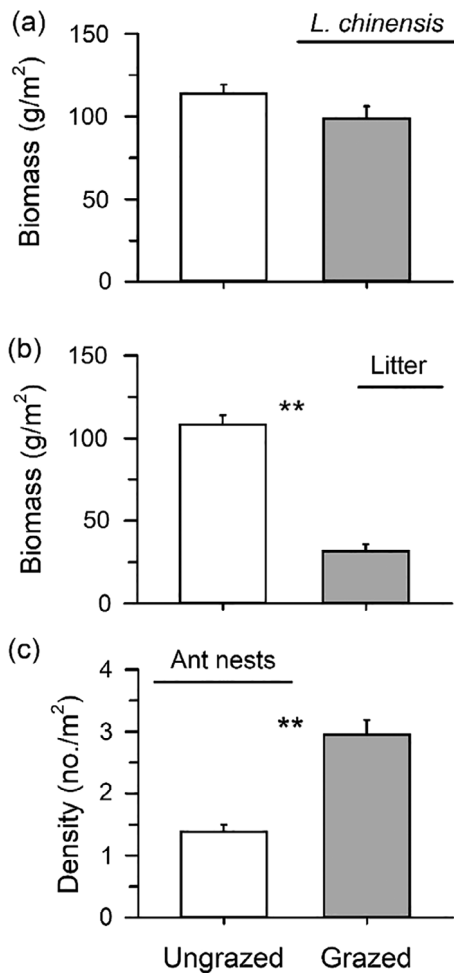


FIGURE 2 Effects of 2 years (2010–2011) of cattle grazing on (a) *Leymus chinensis* biomass, (b) litter biomass, and (c) ant nest density in the medium-scale grazing experiment. Asterisks indicate significant differences (** $p \leq 0.01$). Error bars represent SE

($F_{1,7} = 40.25, p < 0.001$; Table 1, Figure 5b), but did not significantly affect soil moisture, or N or P availability (Table 1).

Indirect effects of ant activities

Pesticide application and fencing to reduce ants led to a significant decrease in *A. scoparia* biomass by 17% ($F_{1,7} = 7.70, p = 0.028$, Figures 4d and 5a) and soil total available N by 15% ($F_{1,7} = 20.85, p = 0.003$, Table 1, Figure 5b), but did not significantly affect soil moisture, light penetration, or P availability (Table 1).

DISCUSSION

Large herbivores can exert profound effects on plant populations through multiple direct and indirect effects that can act simultaneously and are therefore often difficult to distinguish in the field. To our knowledge, our

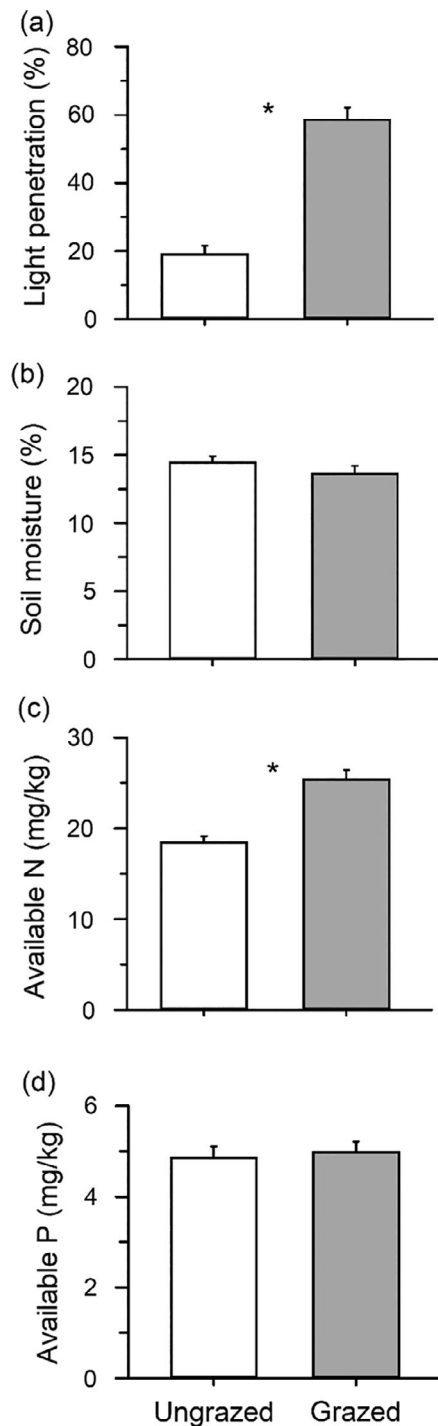


FIGURE 3 Overall effects of 2 years (2010–2011) of cattle grazing on (a) light penetration, (b) soil moisture, (c) soil available N, and (d) soil available P in the medium-scale grazing experiment. Asterisks indicate a significant differences (* $p < 0.05$). Error bars represent SE

study is the first to experimentally tease apart these multiple direct and indirect effects of large herbivores on plants. By integrating a set of medium- and small-scale field experiments, we found that, although cattle commonly consumed *A. scoparia* (in small amounts) in our

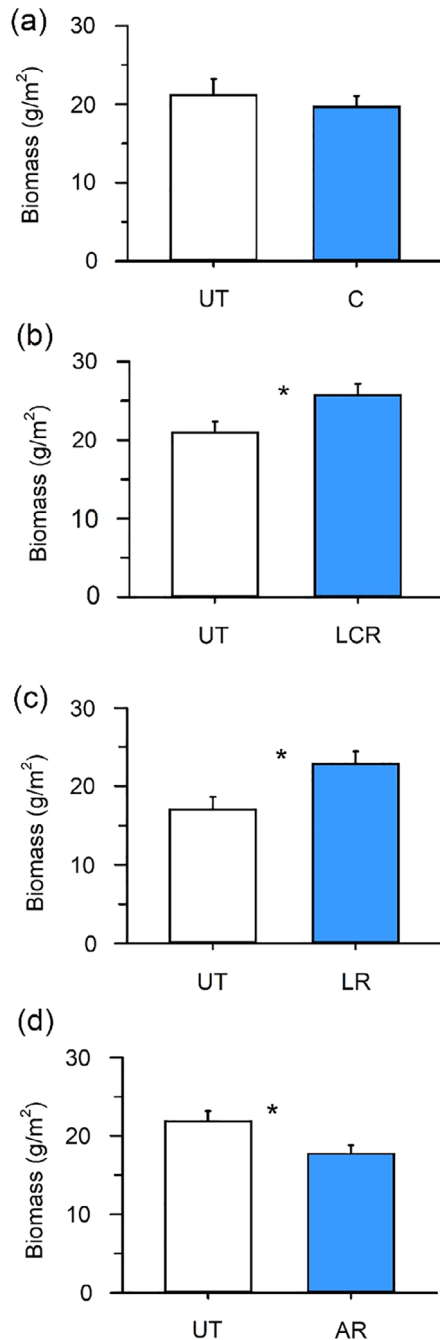


FIGURE 4 Direct (a, consumption) and indirect (b, *Leymus chinensis*; c, litter; and d, ant) effects of cattle on *Artemisia scoparia* biomass in the 2 years (2014–2015) of small-scale experiments. AR, ant reduction; C, consumption; LCR, *L. chinensis* reduction; LR, litter reduction; UT, untreated. Asterisks indicate a significant differences (* $p < 0.05$). Error bars represent SE

study, its biomass actually increased significantly in response to grazing (Figure 1a). This effect occurred because the multiple indirect positive effects of cattle outweighed the direct negative effects of consumption. Our results agree with the hypothesis that several herbivore-driven indirect effects are responsible for the increased

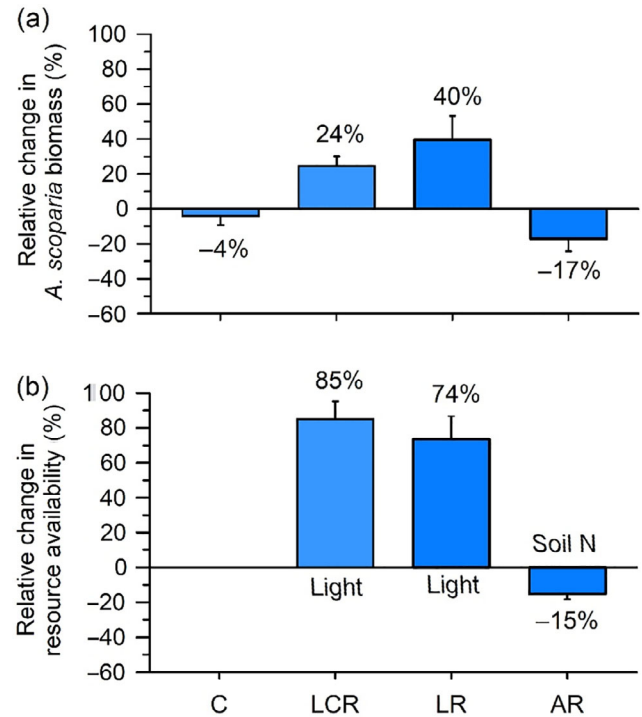


FIGURE 5 A comparison of the effect size (determined as the relative change in a variable, see details in *Data analyses*) of the direct (consumption) and indirect (*Leymus chinensis*; litter; and ant) effects of cattle on (a) *Artemisia scoparia* biomass and (b) resource availability in the 2 years (2014–2015) of small-scale experiments. The effect sizes on resource availability are shown only for those with significant responses to experimental treatments (i.e., understory light penetration and soil N availability). AR, ant reduction; C, consumption; LCR, *L. chinensis* reduction; LR, litter reduction. Error bars represent SE

A. scoparia biomass. Notably, although single indirect effects of large herbivores on plant growth, biomass, and community composition have been widely described (Augustine & McNaughton, 1998; Goheen et al., 2004; Pringle et al., 2011; Veen et al., 2012), our study demonstrates that large herbivores can affect plants by inducing multiple indirect effects simultaneously (also see Goheen et al., 2010).

While herbivores can affect plants via both direct and indirect pathways, separating the relative contributions of these multiple types of interactions in the field remains a challenge. By combining medium- and small-scale experiments, we were able to effectively tease apart the different effects of cattle and quantified their relative strengths in this system. We found that each of the three indirect pathways, namely cattle-induced decreases in *L. chinensis* and litter and increased ant nest density, led to a 24%, 40%, and 17% (indicated by the decreases in plant biomass in the AR treatment) increase in *A. scoparia* biomass (Figure 5a),

respectively. The three positive effects together outweighed the direct, but small, negative effects (4% reduction in biomass) of cattle consumption on *A. scoparia* (Figure 5a). These observed effects were consistent with the overall increase in the growth and biomass of this forb in the presence of cattle that was observed in the medium-scale grazing experiment (Figure 1). These results support the hypothesis that cattle exerted indirect effects on *A. scoparia* growth via their influence on plant competitors, litter, and ants (Figure 2).

These indirect effects were associated with explicable changes in resource availability induced by cattle grazing. Thus, changes in resource availability may be the primary mechanism by which herbivores indirectly affected plants. For *L. chinensis*, while we detected only a marginally significant reduction in its biomass in the grazed plots in the medium-scale grazing experiment (Figure 2a), our small-scale simulated grazing experiment showed that such a mild reduction in plant competition increased light availability by 85% (Figure 5b, Table 1), and was associated with an increase in *A. scoparia*

biomass by 24% (Figure 5a). These results are in line with other studies showing that herbivore-induced changes in light availability can have profound effects on plant interactions and population size through time (Augustine et al., 2017; Borer et al., 2014; Howison et al., 2015; Huisman & Olff, 1998). In addition to light, the release of competition for other key limiting resources such as soil nutrients and water after *L. chinensis* removal by cattle may also be crucial in explaining the positive responses of *A. scoparia* forb (see Augustine et al., 2017).

For plant litter, the accumulation of thick litter at ground surface have been widely reported to suppress seedling germination and growth via their reduction in light penetration and as a physical barrier to seedling emergence (Carson & Peterson, 1990; Facelli & Pickett, 1991; Liu et al., 2018). The removal of litter by cattle in our system likely benefited the germination and growth of *A. scoparia* (Figures 4c and 5a) via the increases of light penetration in the early growing season (Figure 5b, Table 1, also see Liu et al., 2018). Moreover, given that the litter accumulated at the soil surface is abundant

TABLE 1 Effects of 2 years (2014–2015) of experimental treatments on above- and belowground resource availability in the untreated (UT) and treatment (AR, ant reduction; C, consumption; LCR, *Leymus chinensis* reduction; LR, litter reduction) plots in August 2015 in the small-scale experiments

Resource	Treatment					Treatment				
	UT	C	LR	F	p	UT	LCR	AR	F	p
Aboveground										
Light penetration (%)	17.88 (3.53)	16.11 (3.61)		1.06	0.336	18.16 (3.87)	33.41 (7.38)		75.74	<0.001
Belowground										
Soil moisture (%)	11.20 (1.83)	11.54 (1.60)		0.44	0.525	11.75 (1.59)	12.06 (1.45)		0.17	0.693
Soil available N (mg kg ⁻¹)	19.13 (2.35)	18.40 (1.94)		0.73	0.419	19.76 (1.88)	20.30 (2.80)		0.34	0.573
Soil available P (mg kg ⁻¹)	4.13 (0.78)	4.45 (0.74)		0.49	0.506	4.56 (0.79)	4.36 (0.88)		0.22	0.647
Aboveground										
Light penetration (%)	20.10 (3.27)		34.14 (5.15)	40.25	<0.001	19.11 (3.67)		18.71 (5.31)	0.031	0.865
Belowground										
Soil moisture (%)	14.68 (3.51)		13.90 (4.85)	0.12	0.737	13.99 (1.40)		14.61 (1.08)	0.970	0.358
Soil available N (mg kg ⁻¹)	17.21 (3.13)		15.41 (3.14)	4.58	0.075	19.38 (2.75)		16.33 (1.82)	20.854	0.003
Soil available P (mg kg ⁻¹)	3.88 (0.89)		3.70 (0.55)	0.74	0.416	4.35 (0.84)		4.06 (0.75)	0.662	0.443

Note: F and p values are derived from one-way ANOVA with blocking and with *df* = 1, 7. Values in boldface indicate a statistically significant effect of experimental treatment (*p* ≤ 0.05). Data are means with SE in parentheses.

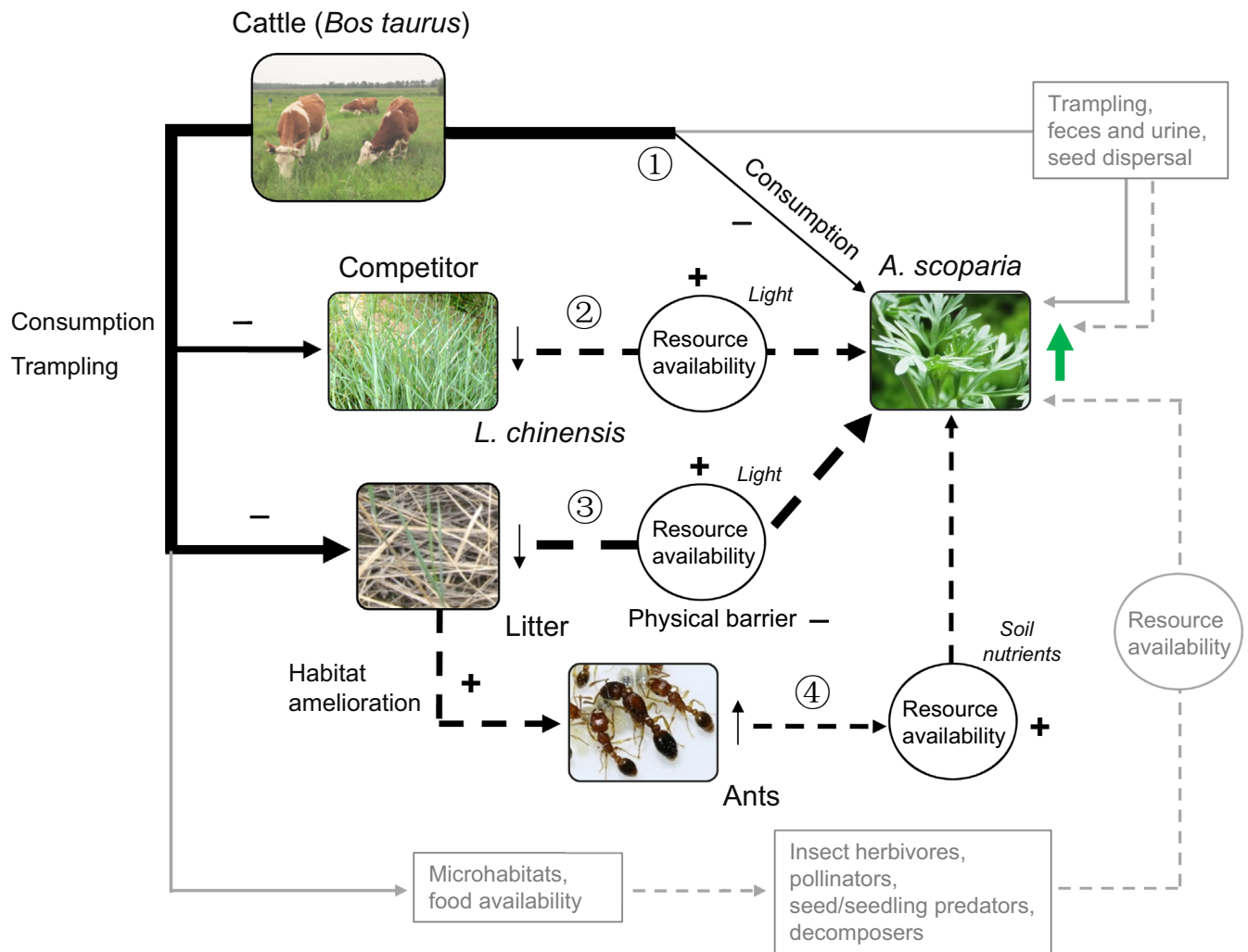


FIGURE 6 Schematic showing the multiple direct (solid lines) and indirect (dashed lines) effects of cattle grazing on the biomass of *Artemisia scoparia*, a dominant forb species, in a temperate grassland in northeast China. (1) direct consumption by cattle had a minor negative effect on *A. scoparia* biomass; (2) cattle-induced decline in *Leymus chinensis* biomass indirectly benefited *A. scoparia* biomass by increasing resource availability; (3) cattle-induced decreases in litter biomass indirectly benefited *A. scoparia* biomass by increasing resource availability and reducing the physical barrier; and (4) cattle-induced increases in ant abundance indirectly benefited *A. scoparia* biomass by enhancing resource availability. A minus sign “-” indicates negative effects; a plus sign “+” indicates positive effects. Italic typeface indicates the types of resources (e.g., light and soil nutrients). We detected a significant change caused by the indirect effects of cattle, potentially contributed to the observed increases in plant growth of *A. scoparia* in the grazed areas. The black arrows indicate decreases or increases in the abundance of competitors, litter, and ants, whereas the green arrow indicates increases in biomass of *A. scoparia*. The thinner black lines indicate the weaker effects, whereas the thicker black lines indicate the stronger effects. The faint solid and dashed lines indicate those direct (e.g., trampling) and indirect effects (e.g., the deposition of animal excreta, changes in pollinators, seed predators, and decomposers) that were not investigated in this study

(e.g., $>150 \text{ g/m}^2$) in the early growing season (e.g., June, see Appendix S1: Figure S5), we suspect that the reduction in physical barrier may also be important in affecting the growth of young *A. scoparia*, though its relative contribution remains to be explored (but see Kostel-Hughes et al., 2005, Liu et al., 2017, Sonkoly et al., 2020). Finally, *A. scoparia* indirectly benefited from increased ant abundance, which significantly enhanced soil N availability in the grazed areas (Figures 4d and 5, Table 1). Ants commonly improve the physical and chemical properties of

soil by their nest-building activities, which in turn increases soil microbial abundance and activities, and thus soil N availability and plant growth (Farji-Brener & Werenkraut, 2017). In addition to soil N availability, the increases in ant abundance may also benefit plant growth by altering soil bulk density, soil moisture, the contents of available P, and other mineral elements (e.g., K and Na; Farji-Brener & Werenkraut, 2017), which might also contribute to the observed increases in plant growth of *A. scoparia* in our system.

One important finding in our study is that large herbivores can exert multiple indirect effects on plants within an ecosystem. The only study we know that investigated multiple indirect effects of large herbivores (Goheen et al., 2010) found that domestic cattle can facilitate seedling establishment of a dominant tree (*Acacia drepanolobium*) in Kenyan savannas by reducing competition from understory grass species and by reducing seed and seedling predation by rodents. Given their large body sizes, energy requirements, and home range sizes, large herbivores can often have profound effects, not only on abiotic conditions, but also on the multiple species with which they interact (Pringle et al., 2007), making the indirect interactions induced by these animals probably more common and complex than previously thought (Forbes et al., 2019; Ohgushi, 2005; Pringle et al., 2011; Rooney & Waller, 2003). Despite the difficulties in detecting multiple indirect effects and documenting their underlying mechanisms, our study shows that a combination of careful field observations and experiments can be effective for revealing such cryptic interactions in the field.

The lack of a strong direct grazing effect on *A. scoparia* in our ecosystem can be attributed in part to the relatively low grazing intensity (e.g., less than 50% of aboveground biomass was removed), and the fact that *A. scoparia* is a less-preferred plant species (e.g., with only about 20% grazing frequency) compared to *L. chinensis*. However, if the intensity of grazing were to increase, cattle might feed more intensely on the less-preferred *A. scoparia*. Thus, we expect that the strength of direct and indirect effects of cattle in this system will be driven at least partially by density as well as dietary preferences of herbivores (also see Augustine & McNaughton, 1998). In addition, compensatory regrowth of plants after herbivory (Hamilton & Frank, 2001; McNaughton, 1983; Zhong et al., 2021) may also mitigate the negative impacts of herbivory and thus lead to neutral responses of *A. scoparia* to grazing (Figure 4a).

In nature, the growth and abundance of plants may be regulated simultaneously by a diverse array of direct and indirect pathways (reviewed by Augustine & McNaughton, 1998). We have focused on a few pathways, but acknowledge that other direct and indirect effects of large herbivores on the target forb species may be operating in our study system. These may include direct negative effects such as trampling (Schrama et al., 2013; van der Wal & Brooker, 2004), and indirect effects such as the deposition of animal excreta (Augustine & McNaughton, 2006; Day & Detling, 1990; Frank et al., 2018; Wang et al., 2018), the influences on insect herbivores (Huntzinger et al., 2008; Rambo & Faeth, 1999; van Klink et al., 2015; Zhong et al., 2017), pollinators (Guy et al., 2021; Vázquez & Simberloff, 2004), seed and seedling predators (Foster et al., 2014; Goheen et al., 2010; Maclean et al., 2011), and

decomposers (Eldridge et al., 2017; Mahon & Crist, 2019; Sankaran & Augustine, 2004). Further investigations are needed to assess the relative importance of these less-studied indirect factors in mediating plant population and communities (see Figure 6).

In conclusion, our study demonstrates that large herbivores (cattle) can affect plant growth and density via multiple indirect effects (also see Strauss [1991] for indirect interactions in animal communities), in addition to the more-acknowledged direct effects of consumption. We show that the positive influences of these multiple indirect effects can override the negative effects of consumption, leading to overall positive impacts on the growth of a target plant species. Globally, large herbivores are facing dramatic shifts in their abundance and distribution due to climate changes and human activities (Bakker & Svenning, 2018; Owen-Smith, 2010; Ripple et al., 2015), and these changes will undoubtedly have important but poorly understood consequences for the prevalence and strength of their direct and indirect effects in terrestrial ecosystems. Focusing on the causes and consequences of herbivore-induced indirect effects, as well as the factors that determine their frequency and importance, will not only help us to better understand the role that these animals play in shaping terrestrial landscapes, but will also lead to more effective land management and conservation practices.

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CONFLICT OF INTEREST

All authors certify that they do not have any conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT


Data (Zhong et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.rfj6q57bt>

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SUPPORTING INFORMATION

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