

Ecosystem carbon exchange in response to locust outbreaks in a temperate steppe

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Abstract It is predicted that locust outbreaks will occur more frequently under future climate change scenarios, with consequent effects on ecological goods and services. A field manipulative experiment was conducted to examine the responses of gross ecosystem productivity (GEP), net ecosystem carbon dioxide (CO₂) exchange (NEE), ecosystem respiration (ER), and soil respiration (SR) to locust outbreaks in a temperate steppe of northern China from 2010 to 2011. Two processes related to locust outbreaks, natural locust feeding and carcass deposition, were

mimicked by clipping 80 % of aboveground biomass and adding locust carcasses, respectively. Ecosystem carbon (C) exchange (i.e., GEP, NEE, ER, and SR) was suppressed by locust feeding in 2010, but stimulated by locust carcass deposition in both years (except SR in 2011). Experimental locust outbreaks (i.e., clipping plus locust carcass addition) decreased GEP and NEE in 2010 whereas they increased GEP, NEE, and ER in 2011, leading to neutral changes in GEP, NEE, and SR across the 2 years. The responses of ecosystem C exchange could have been due to the changes in soil ammonium nitrogen, community cover, and aboveground net primary productivity. Our findings of the transient and neutral changes in ecosystem C cycling under locust outbreaks highlight the importance of resistance, resilience, and stability of the temperate steppe in maintaining reliable ecosystem services, and facilitate the projections of ecosystem functioning in response to natural disturbance and climate change.

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Introduction

Migratory locusts are widespread over the world, primarily in Africa, Asia, Australia, and New Zealand (COPR 1982; Chen 1999). Extreme precipitation and temperature events [e.g., droughts, floods, and heat waves (Lima 2007; Stige et al. 2007; Tian et al. 2011)] can lead to the outbreaks of locusts, especially in dry and warm years (Ma et al. 1965), resulting in serious consequences including crop damage, food shortage, and economic loss. With increasing extreme temperature and precipitation events projected under climate change scenarios (Meehl and Tebaldi 2004;

Schär et al. 2004; Schiermeier 2011), locust outbreaks are expected to occur more frequently and result in negative impacts on ecosystem service (Zhang and Li 1999; Wang et al. 2002; Chen et al. 2006; Sun et al. 2010).

In order to control locust outbreaks (Lecoq 2001; Tanaka and Zhu 2005; Sánchez-Zapata et al. 2007), many studies have been conducted to investigate the influences of abiotic and biotic factors [climate, landscape, and plant nitrogen (N) content] on locust outbreaks (Pedgley 1989; Zhang and Li 1999; Todd et al. 2002; Despland et al. 2004; Lima 2007; Stige et al. 2007; Yu et al. 2009; Zhang et al. 2009; Sun et al. 2010; Tian et al. 2011; Cease et al. 2012). The behaviors and dynamics of locusts during and after outbreaks have also well been illustrated over the past decades (Tanaka 2006; Yamagishi and Tanaka 2009; Ott et al. 2012; Topaz et al. 2012). However, the ecological consequences of locust outbreaks have largely been neglected (see Reef et al. 2012). The limited understanding of the impacts of locust outbreaks on ecosystem functions in the breeding areas poses great challenges for the projection and sustainable management of ecosystem service under natural perturbations.

Locust outbreaks may affect ecosystem structure and functioning in two opposite directions. On the one hand, insects that feed on plant aboveground tissues can substantially suppress plant growth (Hoogesteger and Karlsson 1992; Jardon et al. 1994; Coupe and Cahill 2003; Esper et al. 2007; Cobb 2010) and biomass (Schowalter et al. 1986; Brown 1994; Chase 1996; Thompson et al. 1996; Carson and Root 2000; Branson 2010; Branson and Haferkamp 2014) under outbreak conditions, consequently leading to significant declines in ecosystem function. For instance, the depressed plant growth and productivity caused by the outbreaks of mountain pine beetle can suppress forest ecosystem carbon (C) uptake in North America (Kurz et al. 2008a, b; Brown et al. 2010; Clark et al. 2010; Dymond et al. 2010; Stinson et al. 2011). On the other hand, locust carcasses which are rich in nutrients with approximately 12.11 ± 0.16 % N (Hawlena et al. 2012) fall on the soil surface after the outbreaks. As organic detritus, locust carcasses can be easily decomposed by soil microorganisms (Bardgett 2005), releasing available N into the soils for plant uptake (Schimel and Bennett 2004). Increments in soil N availability induced by insect carcass deposition can stimulate plant growth (Yang 2004, 2013) and consequently promote net ecosystem productivity (NEP) (Mattson and Addy 1975; Albani et al. 2010). Nevertheless, the net effects (both direction and magnitude) and duration of locust outbreaks on ecosystem C cycling remain elusive.

Beginning in August 2010, a field manipulative experiment simulating natural locust feeding and carcass deposition was conducted to examine the effects of locust outbreaks on ecosystem C exchange in a temperate steppe of

northern China. The grassland represents the typical vegetation of the regional grassland biome across the Eurasian continent and is N limited (Niu et al. 2010). The specific objectives of this study were to address: (1) whether and to what extent locust outbreaks affect ecosystem C balance, and (2) how long do the impacts of locust outbreaks on ecosystem C cycling last in the temperate steppe?

Materials and methods

Study site

This study site is located in a semiarid temperate steppe in Duolun County ($42^{\circ}02'N$, $116^{\circ}16'E$, 1,324 m a.s.l.), Inner Mongolia, China. The long-term mean annual temperature and precipitation are 2.2 °C and 379 mm, respectively (China Meteorological Data Sharing Service System). The sandy soil at this study site is classified as a Haplic Calcisol (FAO classification). The dominant species of migratory locusts in this temperate steppe are *Dasyhippus barbipes*, *Oedaleus decorus asiaticus*, *Calliptamus abbreviatus*, *Bryodemus luctuosus luctuosus*, *Angaracris barabensis*, *Myrmeleotettix palpalis*, and *Stenobothrus dubius* (Liu and Guo 2004).

Experimental design

We used a randomized complete block design with six treatments and three replicates for each treatment. Eighteen 1-m \times 1-m plots were arranged into three rows and six columns with a 1-m buffer zone between any two adjacent plots. One of the six plots in each row was randomly assigned to one of the six treatments: control, locust carcass addition of 200 individuals m^{-2} (LC1), locust carcass addition of 400 individuals m^{-2} (LC2), clipping (CL), clipping plus LC1 (CLLC1), and clipping plus LC2 (CLLC2). All the plots were kept open to minimize disturbance during the experimental period. In this area, natural locust densities were approximately 20 individuals m^{-2} under non-outbreak conditions (Li 2007). However, the population densities of locusts could be as high as 50–300 and 30–420 m^{-2} during the outbreaks that generally occur from late July to early August in Inner Mongolian grasslands (Liu and Guo 2004; Chen et al. 2006). This study simulated a locust outbreak event occurring in early August, and took into consideration two factors of locust outbreaks: locust feeding and carcass deposition. We mimicked natural locust feeding by clipping 80 % of plant aboveground biomass on 1 August 2010. According to a preliminary experiment, 81.4 ± 1.5 % of aboveground biomass was removed when plants were clipped at a height of 4 cm above the soil surface (Table S1). Moreover, three levels of locust carcasses:

0, 200, and 400 locust carcasses m^{-2} were added to simulate natural locust carcass deposition on 5 August 2010. The method mimicking insect carcass deposition has been used and validated by two previous studies (Yang 2004, 2013).

Ecosystem C exchange measurements

Ecosystem carbon dioxide (CO_2) exchange was measured with a transparent chamber ($0.5 \times 0.5 \times 0.5 \text{ m}^3$) connected to a LI-6400 (LI-COR, Lincoln, NE). More than 90 % of photosynthetically active radiation could pass the polyethylene sheeting used for the transparent chamber construction. The chamber was sealed to the surface of an iron frame, which was inserted into the soil at 3-cm depth in each plot. Two small fans ran continuously to mix the air within the chamber. Steady-state conditions were achieved inside the chamber after 2 min, and nine consecutive logs of CO_2 concentrations were subsequently recorded at 10-s intervals on each frame during a 90-s period. The increases in air temperature within the chamber were less than $0.2 \text{ }^\circ\text{C}$ during the 90-s period. The rate of CO_2 concentration that draws down or builds up over time during the measurements was used to calculate net ecosystem CO_2 exchange (NEE). The detailed information of these static-chamber flux calculations is presented in the soil flux calculation procedure in the Li 6400 manual (LI-COR 2004). Following the measurements of NEE, the chamber was vented, covered with an opaque cloth, and put back on the same iron frame. The CO_2 exchange was measured again to calculate ecosystem respiration (ER) rate as light was eliminated (and hence photosynthesis). Positive NEE values represented net C loss, while negative NEE values represented net C uptake. Gross ecosystem productivity (GEP) was calculated as the difference between NEE and ER.

One polyvinyl chloride polymer collar (5 cm in height and 10 cm in internal diameter) was permanently inserted 3 cm into the soil in each plot. A soil CO_2 efflux chamber attached to a LI-8100 (LI-COR) was placed on each collar for 1–2 min to measure soil respiration and then moved to the next collar. The aboveground parts of living plants inside the collars were removed by hand at least 1 day before measuring soil respiration. Ecosystem C exchange including GEP, NEE, ER, and SR was measured three times per month between 0900 and 1030 hours on clear, sunny days from August to October 2010 and over the growing season (May–October) in 2011. Since this study mimicked an outbreak of locusts occurring in summer, the measurements of ecosystem C exchange began in early August 2010, right after setting up the experiment, and continued through the rest of the growing season in 2010 and the whole growing season in 2011.

Soil ammonium–N measurements

We collected soil samples using a soil auger (5 cm in diameter and 10 cm in depth) in each plot on 17 August and 17 September 2010 as well as 8 June 8 and 9 July 2011. After removing roots and stones by sieving with a 2-mm mesh, soil samples were stored in iceboxes. In the laboratory, each soil sample (10 g) was extracted with 50 ml of a 2 M potassium chloride solution on a shaker for 60 min. The extracts were analyzed for the concentration of soil ammonium N ($\text{NH}_4\text{-N}$) (Smart Chem 200 Discrete Auto Analyzer; Systea, Italy).

Plant growth and biomass

A visual evaluation method was used to assess plant community cover in August 2011. During the measurements, a 1-m \times 1-m frame with 100 equally distributed grids (10 cm \times 10 cm) was placed above the community canopy in each plot. The cover of each plant species was recorded in all the grids and summed as the species cover in each plot. The covers of all the species were summed as the community cover.

All aboveground plant materials (including standing litter, ground litter, and living aboveground biomass) from one 1-m \times 0.15-m quadrat in each plot were clipped at peak biomass in late August 2011, oven-dried at $65 \text{ }^\circ\text{C}$ to constant weight, and weighed. Standing litter and living aboveground biomass for all the plant species were summed as aboveground net primary production (ANPP).

Data analysis

Repeated-measures ANOVAs (RM-ANOVAs) were used to examine the effects of clipping and locust carcass addition on ecosystem C exchange and soil $\text{NH}_4\text{-N}$ across all the sampling dates in 2010 and 2011. Two-way ANOVAs were performed for community cover and ANPP in 2011. One-way ANOVAs were used for ecosystem C exchange and soil $\text{NH}_4\text{-N}$ across all the sampling dates in 2010 and 2011, as well as community cover and ANPP in 2011, to investigate the net effects of experimental locust outbreaks (i.e., clipping plus locust carcass addition). Simple linear regressions were performed to examine the correlations of ecosystem C exchange with soil $\text{NH}_4\text{-N}$, community cover, and ANPP. Stepwise multiple linear regressions were used to examine the relationships of ecosystem C exchange with abiotic (soil $\text{NH}_4\text{-N}$) and biotic (community cover and ANPP) factors. All statistical analyses were conducted with SAS 9.0 (SAS Institute, Cary, NC).

Results

Effects of experimental locust outbreaks on ecosystem C exchange

Across all the sampling dates in 2010 and 2011, clipping reduced GEP, NEE, ER, and SR by 16.9, 21.1, 9.0, and 14.8 %, respectively (all $P < 0.01$). Under the locust carcass addition, GEP, NEE, ER, and SR increased by 19.6, 18.2, 21.7, and 14.4 % at the LC1 density, and 28.7, 34.2, 29.0, and 14.3 % at the LC2 density, respectively (all $P < 0.01$; Fig. 1; Table 1). No interactions of clipping with locust carcass addition on GEP, NEE, ER, or SR were detected (all $P > 0.05$; Table 1). Compared to the control, experimental locust outbreaks (clipping plus locust carcass addition) did not affect GEP, NEE, or SR under either of the two locust carcass densities (one-way ANOVA, all $P > 0.05$; Fig. 1a, b, d). In addition, experimental locust outbreaks had no impact on ER at the LC1 density ($P > 0.05$), but stimulated it by 15.7 % at the LC2 density ($P < 0.05$; Fig. 1c). When analyzed separately by year, clipping significantly decreased GEP, NEE, ER, and SR in 2010 by 38.1, 51.7, 19.3, and 22.8 %, respectively (all $P < 0.001$; Fig. 2a, c, e, g), but not in 2011 (all $P > 0.05$; Fig. 2b, d, f, h). By contrast, locust carcass addition enhanced GEP, NEE, and ER

by 10.5, 3.3, and 16.3 % at the LC1 density, and 18.1, 20.1, and 21.9 %, respectively, at the LC2 density in 2010 (all $P < 0.05$; Fig. 2a, c, e). In 2011, GEP, NEE, and ER were stimulated by 20.2, 28.6, and 25.1 % at the LC1 density, and 38.8, 40.6, and 33.3 % at the LC2 density, respectively (all $P < 0.01$; Fig. 2b, d, f). Locust carcass addition markedly enhanced SR in 2010 by 17.3 and 24.4 % at the LC1 and LC2 densities, respectively ($P < 0.01$; Fig. 2g), but had no effect on SR in 2011 ($P > 0.05$; Fig. 2h; Table 1). Clipping and locust carcass addition did not interact to affect GEP, NEE, ER, or SR in either year (all $P > 0.05$; Fig. 2; Table 1). In comparison with the control, experimental locust outbreaks suppressed GEP by 35.3 and 57.6 % in 2010 (one-way ANOVA, both $P < 0.05$; Fig. 2a, c), but stimulated it by 26.5 and 42.2 % in 2011 at the LC1 and LC2 densities, respectively (both $P < 0.05$; Fig. 2b, d). Similarly, NEE was reduced by 22.8 and 35.1 % in 2010 (both $P < 0.05$; Fig. 2a, c), but enhanced by 32.9 and 40.0 % in 2011 at the LC1 and LC2 densities, respectively (both $P < 0.05$; Fig. 2b, d). ER did not change in 2010 (both $P > 0.05$; Fig. 2e), but was enhanced by 24.4 and 28.5 % in 2011 at the LC1 and LC2 densities, respectively (both $P < 0.05$; Fig. 2f), under experimental locust outbreaks. Experimental locust outbreaks had no impact on SR irrespective of the locust carcass density or year (all $P > 0.05$; Fig. 2g, h).

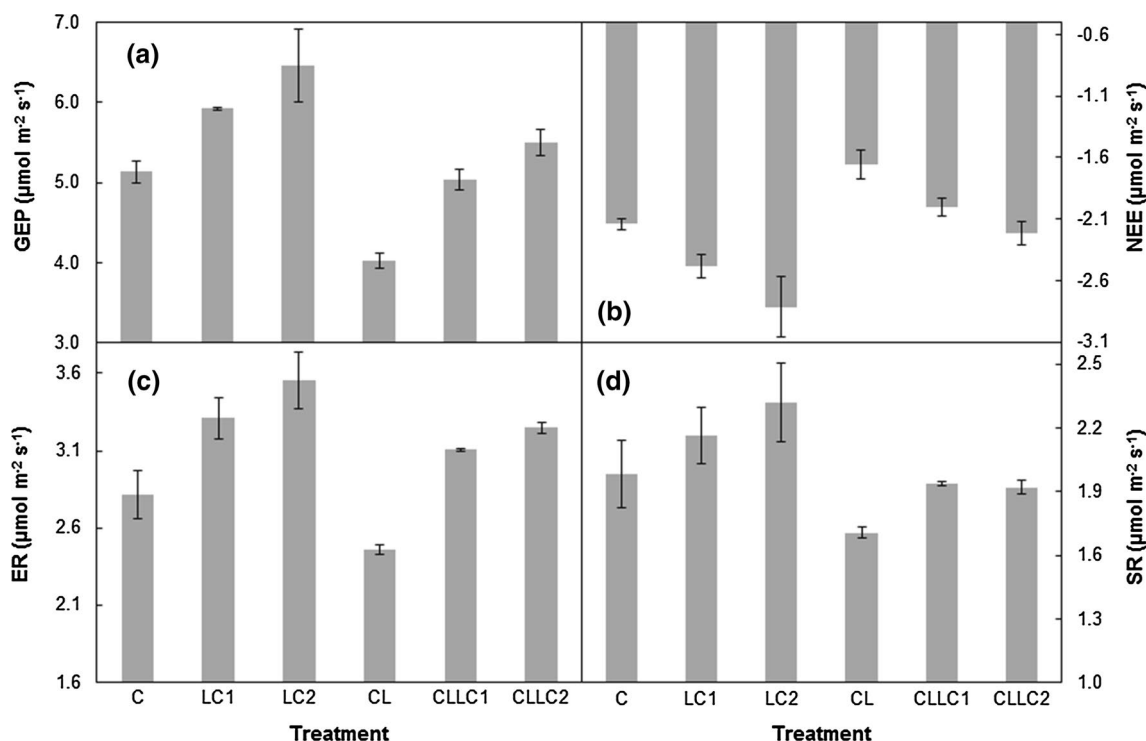


Fig. 1 Mean values of gross ecosystem productivity (GEP; **a**), net ecosystem CO₂ exchange (NEE; **b**), ecosystem respiration (ER; **c**), and soil respiration (SR; **d** means \pm 1 SE) across all the sampling dates in 2010 and 2011; $n = 3$. C Control, LC1 locust carcass addition of 200 individuals m⁻², LC2 locust carcass addition of 400 individuals m⁻², CL clipping, CLLC1 clipping plus LC1, CLLC2 clipping plus LC2

Table 1 Results (*F*-values) of repeated-measures ANOVA on the effects of clipping (*CL*), locust carcass addition (*LC*), sampling date (*D*), and their interactions on gross ecosystem productivity (*GEP*), net ecosystem carbon dioxide exchange (*NEE*), ecosystem respiration (*ER*), and soil respiration (*SR*) across all the sampling dates (mean) in 2010 and 2011

	GEP	NEE	ER	SR
Mean				
CL	43.62***	21.27***	17.11**	12.97**
LC	41.31***	12.44**	22.91***	4.51*
CL × LC	0.38	0.50	0.09	0.19
D	516.07***	158.68***	403.76***	240.71***
D × CL	14.21***	8.09***	5.92***	6.35***
D × LC	10.18***	3.56***	5.13***	4.39***
D × CL × LC	1.61**	1.31 [†]	1.46*	1.82***
2010				
CL	297.42***	255.14***	45.43***	30.73***
LC	14.01***	4.93*	3.89*	8.74**
CL × LC	0.72	1.13	0.27	0.81
D	209.42***	56.67***	169.03***	291.30***
D × CL	36.58***	25.54***	9.97***	10.73***
D × LC	3.13***	2.27**	0.92	7.76***
D × CL × LC	1.48 [†]	1.37	0.47	2.26***
2011				
CL	0.26	0.31	0.95	1.30
LC	40.36***	11.30**	47.24***	1.26
CL × LC	1.18	1.36	0.70	0.05
D	573.13***	176.88***	461.70***	248.38***
D × CL	2.76***	0.96	1.71*	2.74***
D × LC	11.23***	3.61***	5.98***	2.74***
D × CL × LC	1.57*	1.22	1.74*	1.73**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, [†] $P < 0.10$

Treatment effects on soil NH₄-N

Across all the sampling dates in 2010 and 2011, clipping marginally decreased soil NH₄-N by 10.4 % (RM-ANOVA, $P = 0.05$). Locust carcass addition stimulated soil NH₄-N by 85.8 and 144.6 % at the LC1 and LC2 densities, respectively ($P < 0.001$). Significant interaction of clipping with locust carcass addition on soil NH₄-N was found ($P < 0.05$). Compared to the control, experimental locust outbreaks increased soil NH₄-N by 36.6 and 112.7 % at the LC1 and LC2 densities, respectively (both $P < 0.05$, one-way ANOVA). When analyzed separately by year, clipping reduced soil NH₄-N by 14.3 % in 2010 ($P < 0.05$; Fig. 3a), but not in 2011 ($P > 0.05$; Fig. 3b). Locust carcass addition enhanced soil NH₄-N by 106.8 and 173.2 % in 2010 ($P < 0.001$; Fig. 3a), and 33.7 and 73.5 % in 2011 ($P < 0.001$; Fig. 3b) at the LC1 and LC2 densities, respectively. There was a significant interaction between clipping and locust carcass addition in affecting soil NH₄-N in

2010 ($P = 0.01$). In comparison with the control, experimental locust outbreaks did not affect soil NH₄-N at the LC1 density (one-way ANOVA, $P > 0.05$), but significantly increased soil NH₄-N by 125.1 % at the LC2 density in 2010 ($P < 0.05$; Fig. 3a). In 2011, soil NH₄-N was enhanced by 44.2 and 74.0 % at the LC1 and LC2 densities, respectively, under experimental locust outbreaks (both $P < 0.05$; Fig. 3b).

Treatment effects on plant cover and productivity

In 2011, clipping had no effect on community cover ($P > 0.05$), but significantly decreased ANPP by 22.8 % ($P < 0.01$; Fig. 4). Locust carcass addition marginally increased community cover by 3.1 and 3.2 % (absolute changes, $P < 0.10$; Fig. 4a), and markedly stimulated ANPP by 76.2 and 96.9 % at the LC1 and LC2 densities, respectively ($P < 0.001$; Fig. 4b). No interactive effect of clipping and locust carcass addition on community cover or ANPP was detected (both $P > 0.05$). Compared to the control, experimental locust outbreaks did not impact community cover irrespective of the density of locust carcass addition, or ANPP at the LC1 density (one-way ANOVA, both $P > 0.05$), but substantially enhanced ANPP by 50.0 % at the LC2 density ($P < 0.05$; Fig. 4).

Relationships of ecosystem C exchange with abiotic and biotic factors

Across all the sampling dates in 2010 and 2011, mean GEP, NEE, ER, and SR increased linearly with increasing soil NH₄-N (Fig. 5a, d) and ANPP (Fig. 5c, f; Table S2). Positive correlations of GEP, ER, SR, but not NEE, with community cover were detected (Fig. 5b, e; Table S2). Stepwise multiple regression analyses demonstrated that soil NH₄-N alone accounted for 62.7 % of the variation in GEP ($P < 0.001$). ANPP was responsible for 53.9 and 43.2 % of the variation in NEE and SR, respectively (both $P < 0.01$). Seventy-eight percent of the variation in ER could be explained by the combination of soil NH₄-N ($R^2 = 0.71$, $P < 0.001$) and ANPP ($R^2 = 0.07$, $P < 0.05$).

Across the 18 plots, seasonal mean GEP, NEE, ER, and SR showed positive dependence upon soil NH₄-N in 2010 (Fig. 6a, e; Table S2). In 2011, positive relationships of mean GEP, NEE, and ER with soil NH₄-N (Fig. 6d), community cover (Fig. 6c), and ANPP (Fig. 6b; Table S2) were found. Seasonal mean SR tended to increase with community cover ($P < 0.10$; Fig. 6g). In 2010, soil NH₄-N alone contributed to 23.0, 45.8, and 35.2 % of the spatial variations in GEP, ER, and SR, respectively (both $P < 0.05$). However, no variable was significantly correlated to NEE. In 2011, soil NH₄-N alone explained 76.9 and 62.8 % of the spatial variations in GEP and NEE, respectively

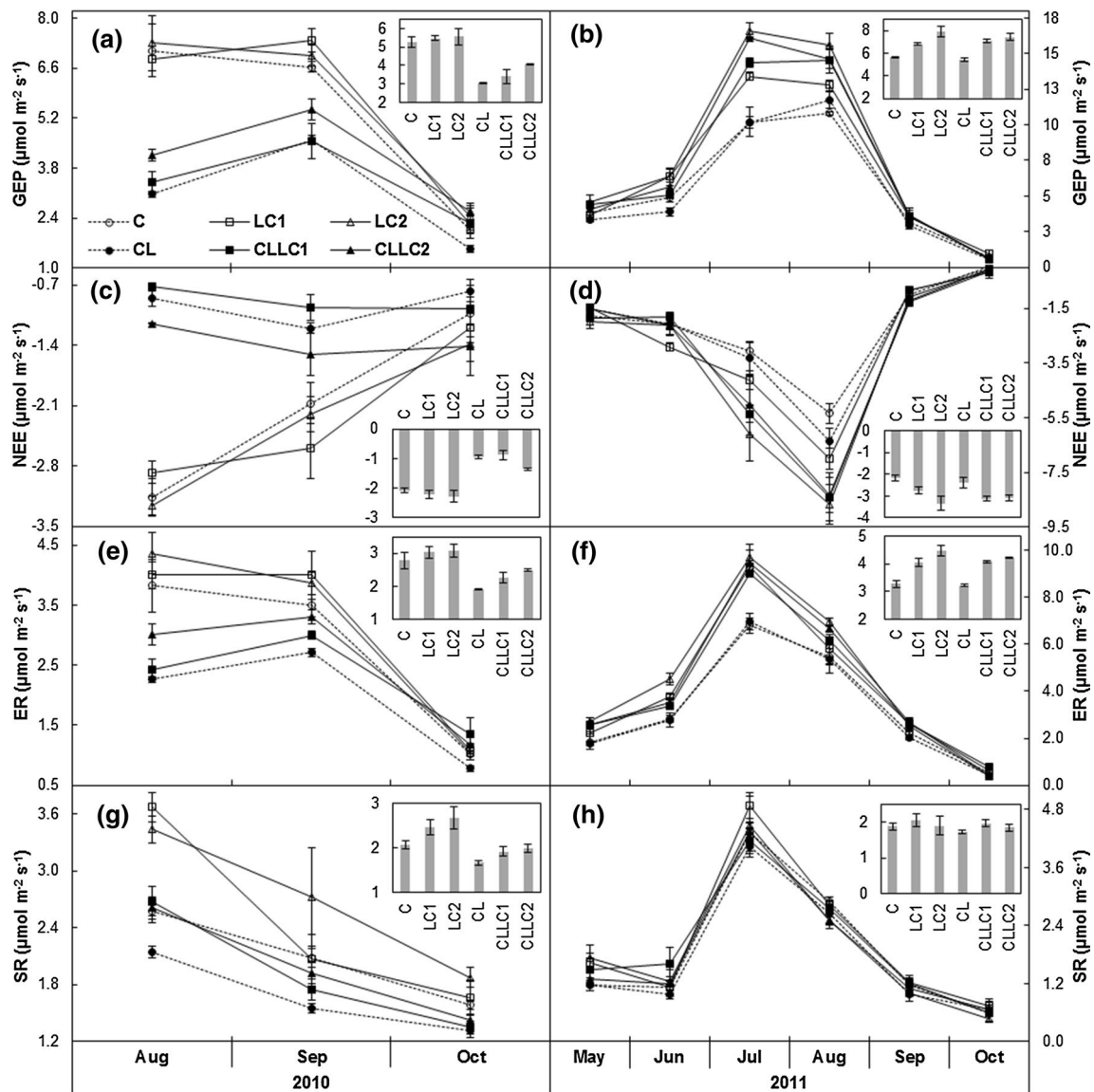


Fig. 2 Seasonal dynamics and means (*insets*, means \pm SE) of GEP (a, b), NEE (c, d), ER (e, f), and SR (g, h) in 2010 (*left panels*) and 2011 (*right panels*). See Fig. 1 for abbreviations

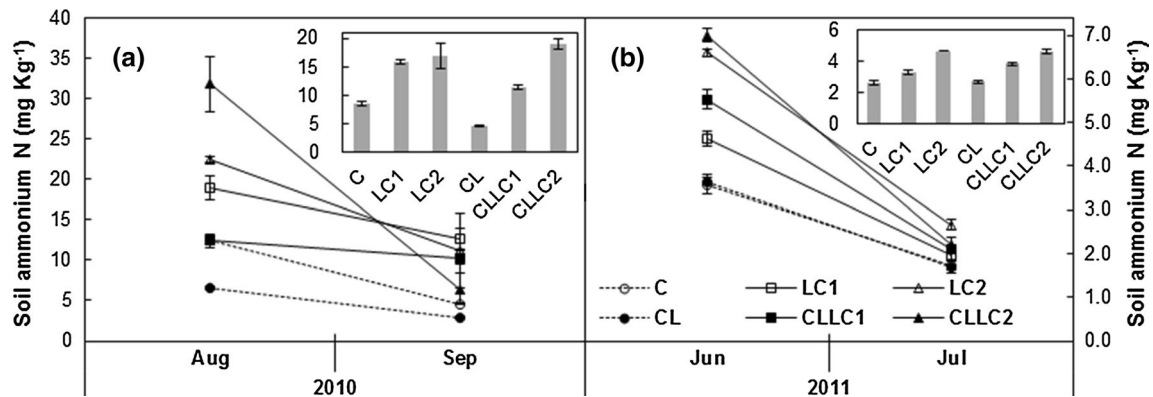


Fig. 3 Treatment effects on soil ammonium N (*insets*, means \pm SE) in a 2010 and b 2011. See Fig. 1 for abbreviations

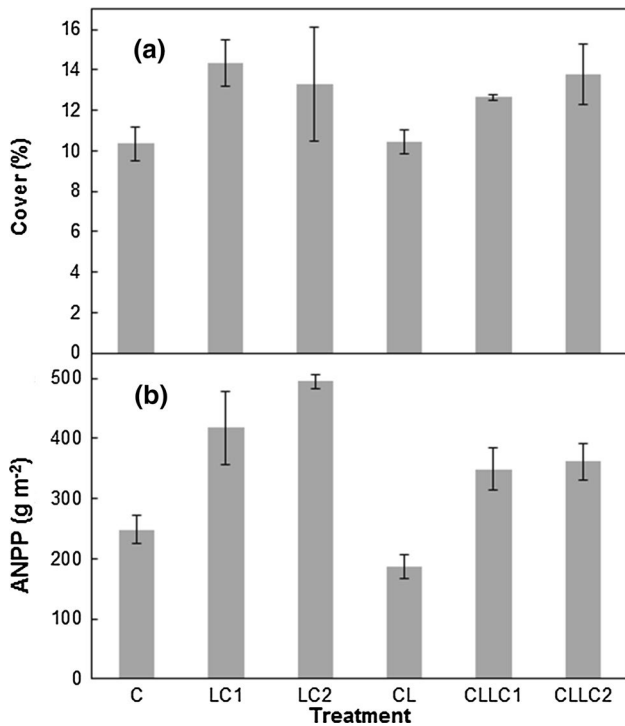


Fig. 4 Treatment effects on community cover and aboveground net primary productivity (ANPP; means \pm 1SE) in 2011. See Fig. 1 for other abbreviations

(both $P < 0.001$). The combination of soil $\text{NH}_4\text{-N}$ (partial $R^2 = 0.70$, $P < 0.001$) and ANPP (partial $R^2 = 0.11$, $P = 0.01$) accounted for 80.6 % of the spatial variations in ER. No variable was found to influence SR.

Discussion

Effects of simulated locust feeding and carcass deposition on ecosystem C exchange

As expected, ecosystem C exchange under clipping was suppressed by 20–50 % in 2010 in the temperate steppe of northern China. Numerous previous studies have demonstrated that, at low density, grasshopper herbivory usually has neutral (Gibson et al. 1990; Whiles and Charlton 2006; Rose et al. 2011) or limited effects on grassland plant growth (biomass loss $< 10\%$) in North America and China (Hewitt et al. 1976; Fry et al. 1978; Hewitt and Onsager 1982; Landsberg and Ohmart 1989; Ritchie and Tilman 1992, 1993; Redak and Capinera 1994; Carson and Root 1999; Coupe and Cahill 2003; Kula et al. 2005; Begna and Fielding 2005, 2008; Orians et al. 2011; Zhang et al. 2011; Suwa and Louda 2012). However, locusts at a similar density could cause more severe damage (30 %

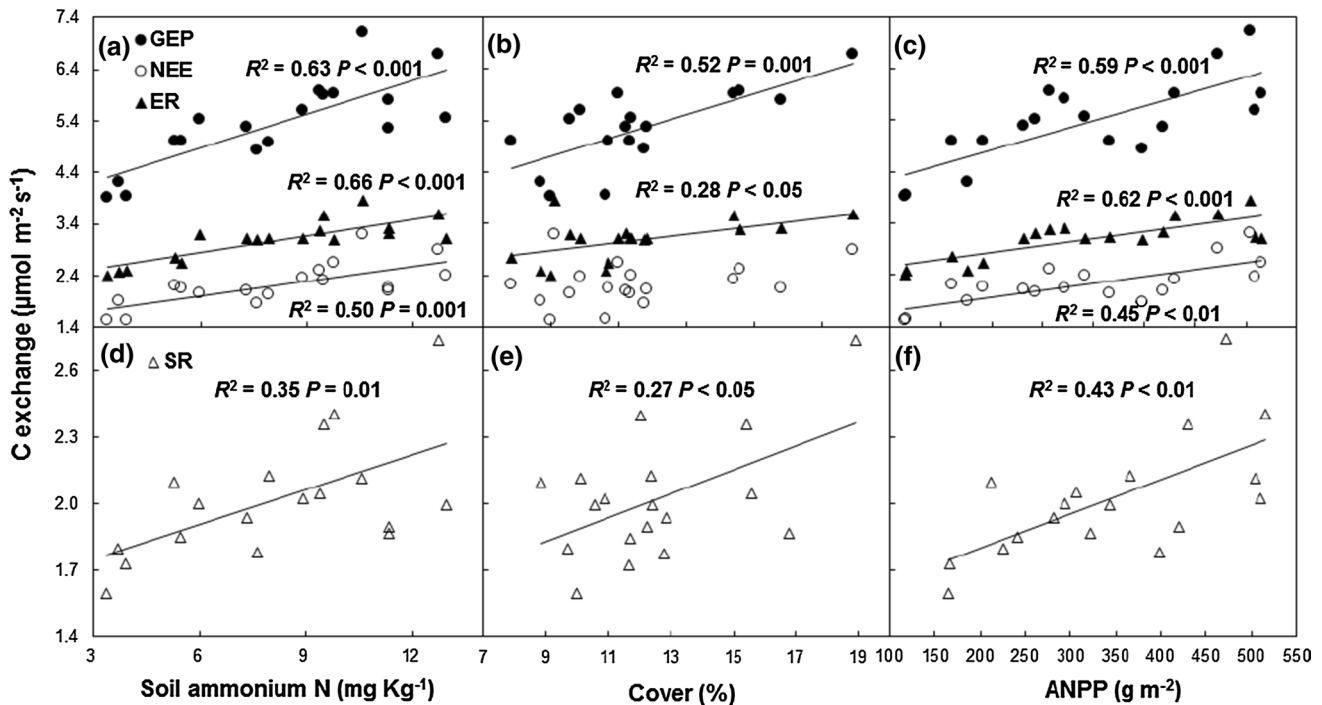


Fig. 5 Dependence of GEP (filled circles), NEE (open circles), ER (filled triangles), and SR (open triangles) on soil $\text{NH}_4\text{-N}$ (a, d), community cover (b, e), and ANPP (c, f). Each data point of GEP, NEE,

ER, and soil $\text{NH}_4\text{-N}$ represents the mean value across the 2 years in one plot. Data for community cover and ANPP are from 2011. See Fig. 1 for abbreviations

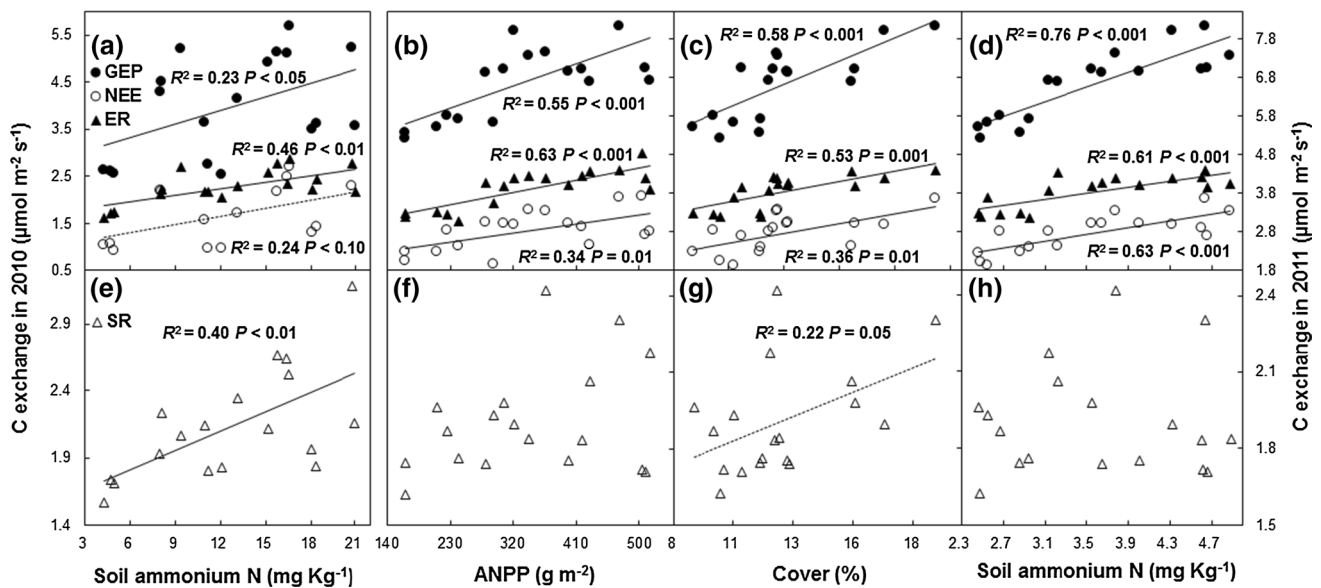


Fig. 6 Dependence of mean GEP (filled circles), NEE (open circles), ER (filled triangles), and SR (open triangles) on soil $\text{NH}_4\text{-N}$ (a, e) in 2010. Dependence of mean GEP, NEE, ER, and SR on soil $\text{NH}_4\text{-N}$

(d, h), community cover (c, g), and ANPP (b, f) in 2011. Each data point represents the mean value in one plot. See Fig. 1 for abbreviations

biomass loss) in plant communities with high species diversity (Scherber et al. 2010), greater legume dominance (Loranger et al. 2014), or at high elevation (Blumer and Diemer 1996). By contrast, Dyer et al. (1993) have found that low-level herbivory under non-outbreak conditions could increase plant production, whereas extremely high-intensity herbivory under outbreak conditions results in substantial productivity reduction. At outbreak density, grasshopper herbivory could reduce approximately 70–95 % of the aboveground biomass in short- and mixed-grass prairies (Burlerson and Hewitt 1982; Chase 1996; Thompson et al. 1996; Carson and Root 2000; Branson 2010; Branson and Haferkamp 2014). Therefore, clipping 80 % of aboveground biomass in this study could well have simulated biomass losses caused by locust feeding under outbreak conditions.

Severe biomass losses and the reduction in soil $\text{NH}_4\text{-N}$ could be responsible for the depressed ecosystem C exchange in 2010. Nevertheless, little changes in ecosystem C exchange in 2011 under the clipping treatment could be accounted for by the relatively lower ANPP in 2011 and the lack of change in soil $\text{NH}_4\text{-N}$ in 2011. These observations suggest that the negative impacts of locust feeding on ecosystem C exchange under outbreak conditions as mimicked by clipping are transient and detectable only in the same growing season. The capability of rapid recovery in this system from the simulated locust feeding under outbreak conditions plays an important role in maintaining ecosystem stability in the temperate grasslands (Amiro et al. 2010).

In the temperate steppe, the increments in ecosystem C exchange under the locust carcass deposition could have been due to the stimulated soil $\text{NH}_4\text{-N}$, community cover, and ANPP in both years. The enhancements of soil $\text{NH}_4\text{-N}$, community cover, and ANPP under the locust carcass addition are in agreement with several previous studies on insect carcass deposition (Seastedt and Tate 1981; Carlton and Goldman 1984; Hollinger 1986; Nowlin et al. 2007; Yang 2004, 2013). The observations suggest that the deposition of locust carcasses after outbreaks can substantially increase ecosystem C cycling via relieving soil N limitation and promoting plant growth and productivity in the N-limited temperate steppe. These findings are in accordance with those in a cicada litterfall (Yang 2004) and a carcass synthesis study (Barton et al. 2013), which have found that carcass deposition can create “bottom-up” effects on aboveground ecosystem functioning by modifying belowground nutrient cycling. Differing from the transient impacts of simulated locust feeding, locust carcass deposition enhanced ecosystem C cycling in both years, which could be ascribed to the processes of carcass decomposition and nutrient release into soil and nutrient supply for plant uptake after locust outbreaks.

Net effects of locust outbreaks on ecosystem C cycling of the temperate steppe

As demonstrated here and in previous studies, locust feeding mimicked by clipping and locust carcass

deposition under outbreak conditions have opposite effects on ecosystem C cycling. Thus, the net effects of locust outbreaks on ecosystem C exchange are determined by the relative strengths of these two aspects. In this study, the net effects of locust outbreaks on ecosystem C exchange also varied with time. The negative effects of clipping were greater than the positive impacts of locust carcass addition in 2010, leading to suppression of GEP and NEE under the experimental locust outbreaks. The reductions in NEE in 2010 were mainly caused by the decreases in GEP, as no changes in ER were found under the experimental locust outbreaks. During the outbreak year, the negative responses of NEE to locust outbreaks in the temperate steppe are similar to the marked and rapid decreases in NEE in forest ecosystems caused by insect outbreaks which suppress tree growth and increase tree mortality (Mattson and Addy 1975; Blais 1981; MacLean 1984; Veblen et al. 1991; Kurz and Apps 1999; Lovett et al. 2006; Cook et al. 2008; Kurz et al. 2008a, b; Albani et al. 2010; Amiro et al. 2010; Brown et al. 2010; Clark et al. 2010; Dymond et al. 2010; Stinson et al. 2011). Some studies also found that the effects of insect outbreaks on NEE are minor due to the similar reductions in both GEP and ER (Moore et al. 2013). In 2011, the increments in GEP, NEE, and ER under the experimental locust outbreaks could have been primarily accounted for by the legacy and positive effects of locust carcass addition and the reduced transient negative impacts of locust feeding in the second year. Similar observations have been reported that insect outbreaks reduce NEP during outbreaks but increase NEP in the year after the outbreaks (Mattson and Addy 1975; Cook et al. 2008; Albani et al. 2010; Amiro et al. 2010). The enhanced plant productivity after outbreaks in both grassland and forest ecosystems (Risley and Crossley 1993; Towne 2000; Parmenter and MacMahon 2009) could be primarily attributable to the enhanced decomposition of plant and insect litter and subsequent increase in soil N availability. Moreover, the stimulations in 2011 compensated for the reductions in 2010 under the experimental locust outbreaks, resulting in neutral change in NEE within the 2-year experimental period. These findings indicate that the temperate steppe has strong resistance, resilience, and stability under natural perturbations.

Insect frass could be a source of soil nutrient during insect outbreaks (Hunter 2001). Numerous studies have reported that insect frass inputs can increase soil nutrient availability (Hollinger 1986; Belovsky and Slade 2000; Hunter 2001; Frost and Hunter 2004; Fonte and Schowalter 2005; Schowalter et al. 2011) and subsequently stimulate plant growth and ecosystem C cycling. In addition, locusts are messy eaters and create lots of greenfall. Both frass and greenfall are labile substrates for decomposition and can

contribute substantially to ecosystem C cycling. Therefore, the removal of aboveground green biomass from the plots by clipping and the addition of locust carcasses without in situ activities of living locusts in the plots neglect the role of greenfall and frass in regulating ecosystem C cycling, thus this work might have underestimated the responses of ecosystem C cycling to locust outbreaks in the semiarid grasslands.

It has well been documented that the locust outbreaks are often triggered by drought in many regions (Lima 2007; Stige et al. 2007; Tian et al. 2011). In addition, ecosystem C fluxes could be suppressed by plant stress resulting from water limitations (Xia et al. 2009). However, the study site experienced a severe drought in 2009 and normal precipitation in 2010 and 2011. Thus, caution should be taken when extrapolating our findings to the regional scale or other grasslands. Further studies need to be conducted to examine the combined effects of drought and locust outbreaks on ecosystem C exchange.

Conclusion

This study investigated the responses of ecosystem C exchange to locust outbreaks by simulating locust feeding with clipping 80 % of aboveground biomass, and locust carcass deposition with the manual additions of locust carcasses in a temperate steppe of northern China. The compensation of the clipping-induced reductions in GEP and NEE by the locust carcass addition-induced stimulations, as well as the suppressions of GEP and NEE in 2010 and the enhancements in 2011, lead to the neutral changes in ecosystem C uptake over the 2-year experimental period. The strong resistance, resilience, and stability under natural perturbations ensure the capability of the temperate steppe in providing reliable ecological service. Our findings can improve the mechanistic understanding of ecosystem C cycling in response to locust outbreaks in temperate steppe ecosystems and facilitate the projections of ecosystem function under natural perturbations in the future.

Author contribution statement Shiqiang Wan conceived and designed the experiments. Dandan Wu, Pengshuai Shao, and Jian Song performed the experiments. Jian Song, Shiqiang Wan, and Dafeng Hui analyzed the data and wrote the manuscript.

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