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ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Pocket gopher disturbance slows soil carbon accumulation in abandoned agricultural lands

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Handling Editor:
Samantha K. Chapman

Abstract

Soil carbon (C) sequestration rates vary widely in abandoned agricultural lands, and factors determining this variation, beyond climate, soil type, and productivity, are poorly understood. One such factor is soil disturbance by burrowing mammals. Despite being ubiquitous in all grasslands, the impact of burrowing mammals on soil C dynamics is not well understood. We quantified the major ecosystem processes that are influenced by one such burrowing mammal, plains pocket gophers (*Geomys bursarius*), in old field ecosystems located in east-central Minnesota, USA. We found that pocket gopher abundance varied among old fields and that newly formed gopher mounds covered up to 6% of the soil surface annually. We first measured short-term C pool and flux changes induced by gopher activities. Soil N mineralization did not differ between the soil in gopher mounds and undisturbed soil. However, for the soil under gopher mounds, N mineralization was 30% lower compared with the undisturbed soil. We developed a process model to simulate the long-term gopher disturbance impact on old field soil C accumulation. This simulation showed that pocket gophers reduced both the rate of soil C accumulation and the total C pool. This reduction is primarily driven by reduced plant C input due to the time it requires for the vegetation to recolonize gopher mounds. Soil organic matter (SOM) decomposition changes had only a minor impact. The process model showed that the depth from which burrowing mammals redistribute soil to the surface is a key factor in determining the overall impact on SOM. In total, our study indicated that soil disturbance by burrowing animals could significantly reduce C storage in old field ecosystems when the mammals are mostly active at the surface soil and can be a significant factor in decreasing overall C sequestration after land abandonment. However, at our study site, gopher abundance decreased with abandonment age, which was likely to have been cause by successional vegetation changes, therefore the gopher disturbance-induced reduction in soil C is transient and decreases with abandonment age.

KEYWORDS
abandoned agricultural lands, burrowing mammals, carbon sequestration, ecosystem carbon budget, old fields, soil carbon, soil organic matter modeling

INTRODUCTION

Soil organic matter (SOM) is the largest terrestrial carbon (C) pool, storing more C than is contained in vegetation and the atmosphere combined (Jobbágy & Jackson, 2001; Schlesinger & Bernhardt, 2013). Changes in the SOM are relatively slow, and the C pool in SOM is much more stable than the vegetation and atmospheric pools. Over the last few centuries, conventional agriculture has led to significant SOM losses (Conant et al., 2001; Knops & Tilman, 2000). It has been estimated that the conversion from natural ecosystems to agriculture has depleted SOM by as much as 60% in soils in temperate regions and by 75% in soils in the tropics (Lal, 2004). However, these agricultural-induced SOM losses are not permanent and changes in land use or management can result in SOM pool increases or further decreases.

One such change is agricultural land abandonment (McLauchlan et al., 2006; O'Brien et al., 2010; Post & Kwon, 2000). Despite the expansion of agricultural practice into new areas, there is a growing trend of agricultural land abandonment worldwide (Cramer et al., 2008; Li & Li, 2017; Ustaoglu & Collier, 2018; Yin et al., 2020). It is clear that abandoned agricultural lands (old fields) can accumulate C over time (Post & Kwon, 2000); however, widely varying rates of C accumulation have been reported (McLauchlan et al., 2006). Many studies on C sequestration in old fields have focused on mechanisms involving primary production, climate, and edaphic factors (Knops & Tilman, 2000; McLauchlan et al., 2006; O'Brien et al., 2015) because these factors directly control the inputs and stability of SOM. However, the impact of burrowing mammal activities on long-term soil C accumulation in abandoned agricultural lands is not well understood, even though burrowing mammals are ubiquitous worldwide in grasslands and old fields (Begall et al., 2007; Davidson et al., 2012; Inouye et al., 1987b) and they have a profound influence on soil properties and functions (Decker et al., 2019; Haussmann, 2017; Lindtner et al., 2019; Louw et al., 2019; Mallen-Cooper et al., 2019).

The population density and spatial distribution of burrowing mammals are strongly influenced by human management (Davidson et al., 2012) due to their perceived role in consuming vegetation and competing with livestock. The population of burrowing mammals is commonly reduced in agricultural fields and pastures by poisoning and trapping (Begall et al., 2007). However, populations of burrowing mammals re-establish after agricultural abandonment (Inouye et al., 1987b). Therefore, understanding how burrowing mammals' activities affect SOM dynamics can improve our overall understanding of soil C sequestration after land abandonment.

An example of such a burrowing mammal is the North American pocket gopher (Geomydiae). Pocket gophers can profoundly alter ecosystem C pools (Figure 1) (Inouye
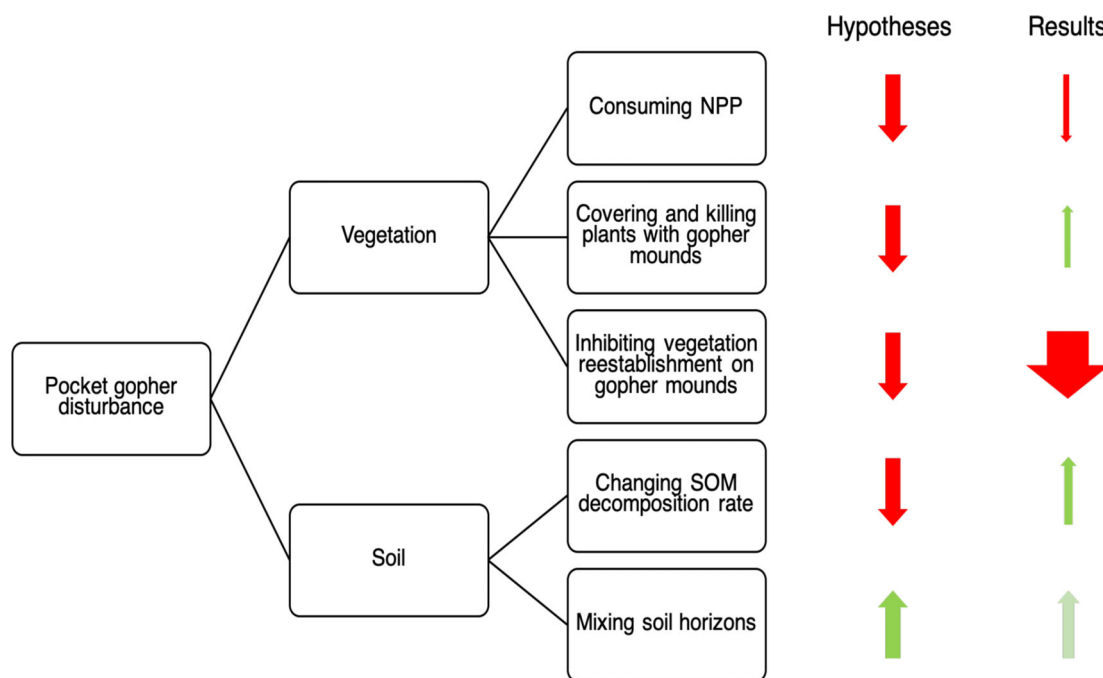

FIGURE 1 Hypotheses and results of the vegetation and soil C fluxes changes induced by pocket gophers. Downward red arrows indicate a decrease of C fluxes, whereas upward green arrows indicate an increase of C fluxes. The arrow size indicates the relative importance of the process in influencing the soil C pool

et al., 1997; Reichman & Seabloom, 2002; Yurkewycz et al., 2014) by influencing both vegetation productivity and soil C dynamics (Huntly & Inouye, 1988). The impact of pocket gophers on vegetation can be separated into three aspects. First, gophers construct extensive tunnel systems, dens, and food caches (Huntly & Inouye, 1988). Building and maintaining the tunnel systems are energetically costly. Vleck (1979) estimated that the cost of tunnel excavation is 360–3400 times as much as walking on the ground surface. Because of this high energy demand, gophers have a high rate of food consumption, which can significantly decrease plant biomass. Second, soil from newly excavated tunnels is transported to abandoned tunnels or to the surface to form mounds, which can cover up to 30% of the surface every year (Hobbs & Mooney, 1985). These gopher mounds bury and kill the vegetation and thereby further reducing primary production. Third, gopher mounds create gaps in vegetation, which might improve germination for certain species and cause vegetation composition changes. However, the mortality of newly germinated seedlings can be high due to exposure to herbivores and dry soil conditions on mounds. As a result, it can require several years for plant biomass on gopher mounds to recover to the level prior to disturbance (Reichman & Seabloom, 2002). Pocket gopher disturbance also affects the decomposition of SOM. The soil in gopher mounds has lower bulk density than the surrounding soil, and therefore has increased aeration and microbial activities, leading to an increase in SOM decomposition and nutrient leaching (Sherrod & Seastedt, 2001; Yurkewycz et al., 2014). In addition, gopher mound production transfers subsurface soil to the surface, which results in a vertical SOM redistribution (Reichman & Seabloom, 2002). In ecosystems with decreasing soil nutrients with deeper soil depth, gopher mound formation can lead to a reduction in C and N in the surface soil (Huntly & Inouye, 1988). Soil that is covered by gopher mounds becomes a subsurface horizon, where the microbial activity is usually lower than that of surface soil (Rumpel & Kögel-Knabner, 2011). Therefore, SOM under mounds could be preserved. Previous research on pocket gopher activities has examined their disturbance effects on vegetation composition (Eviner et al., 2005; Jones et al., 2008; Seabloom & Richards, 2003), nutrient heterogeneity (Huntly & Inouye, 1988; Seabloom et al., 2011), and short-term soil C and N dynamics (Platt et al., 2016; Yurkewycz et al., 2014) separately. However, as far as we know, no study has comprehensively evaluated the impacts of pocket gophers on both soil and vegetation and has simulated gopher impacts on long-term ecosystem C dynamics.

In this study, we examined plains pocket gopher (*Geomys bursarius*) activities in old field ecosystems in east-central Minnesota, to determine if gophers have a

significant impact on soil C pool changes and, if so, the mechanism by which gophers influence soil C pools. As soil C accumulation is a slow process and detecting soil C changes requires decades (Knops & Tilman, 2000), we developed a process-based model to evaluate the long-term effects of gopher disturbance on C dynamics under current management (with or without prescribed burning). We hypothesize that (1) pocket gopher activity decreases soil C inputs due to their plant consumption, which reduces net primary production (NPP), burying vegetation under gopher mounds, and the slow vegetation recolonization on the gopher mounds; (2) gopher disturbance increases SOM decomposition rates, leading to increased C losses; (3) gopher burrowing activities redistribute soil C, which decreases surface soil C and increases subsurface soil C; (4) gopher disturbance reduces the rate of old field soil C accumulation, combining reduced C input and increased C losses; and (5) the gopher impacts on the long-term soil C pool size depends on the intensity of gopher-induced disturbance. The first three hypotheses were tested with empirical data either from field measurements or estimation based on data from published literature. We then constructed a process-based model using the above data as parameters to evaluate the latter two hypotheses.

METHODS

Site description

This research was conducted at the Cedar Creek Ecosystem Science Reserve (CCESR), which is located at East Bethel, Minnesota (USA) (42°25′ N, 93°10′ W). The growing season is from approximately May through August. The soils at CCESR were formed from glacial outwash and the four soil associations identified Nymore, Rifile-Lupton, Sartell, and Zimmerman (Grigal et al., 1974). The old field soils at CCESR were predominantly categorized as Nymore or Zimmerman association, which are both within the Entisol soil order. The native vegetation of Zimmerman soil was oak forest, whereas it was prairie for Nymore soil. Both soil types were dominated by medium and fine sand and had low organic matter contents. The soils were also well drained and aerated (Grigal et al., 1974).

Before European settlement, CCESR was a mosaic of oak savanna, perennial grasslands, upland deciduous forest, and lowland marshes (Cook & Allan, 1992). Cultivation at CCESR started in the late 1800s (Grigal et al., 1974). Common crops grown in this area were corn, potatoes, wheat, rye, and alfalfa. Over the past 90 years, most of the fields were abandoned and vegetation is undergoing natural succession. As field abandonment age

increases, the species composition shifts from dominance by annual forbs to C3 grasses to C4 grasses (Knops & Tilman, 2000; Tilman, 1994). There was tree encroachment in three out of 21 old fields. This study was conducted in 21 old fields that were abandoned during the period 17–87 years before 2014. These fields are part of a long-term chronosequence study (Knops & Tilman, 2000, Tilman, 1994) set up to monitor the vegetation and soil C and N dynamics after agricultural abandonment. Within each field, four permanent, parallel transects (40 m long and 25 m apart) were set up in 1983 for repeated vegetation and soil sampling. Each transect contains 25 1×0.5 m plots (Inouye et al., 1987a). Since 2006, each field has been divided in half, and one-half was randomly chosen for periodic prescribed burning (a fire approximately every other year). Therefore, currently in each field, two transects are in the burned half and the other two are in the unburned half.

C pools and fluxes in the undisturbed soil

Before we constructed the process model to simulate the effect of pocket gopher disturbance on soil C pool changes (Figure 2), we first estimated the annual ecosystem C pools and fluxes in the undisturbed soil in order to acquire and validate parameters such as total annual C input and soil C decomposition fraction. Vegetation, soil C pool, and soil efflux data were collected in 2012 in the biodiversity, CO_2, and nitrogen (BioCON) experiment at CCESR. BioCON is a three factorial experiment designed to examine how elevated CO_2, N deposition, and biodiversity affect ecosystem functions. Pocket gophers are actively removed from the entire BioCON old field, therefore the BioCON soil data reflect soil dynamics in the absence of pocket gophers. Detailed experimental designs are described in Isbell et al. (2018). BioCON data were used because the experiment is located in one of the old fields at CCESR, and this field is representative of the climate condition and soil characteristics of the old fields used in this study. In addition, all essential C fluxes have been collected extensively in BioCON, whereas other old fields lack detailed data, such as soil efflux, root growth, and soil temperature. The BioCON experiment includes 296 2 m $\times$ 2 m plots in six 20-m diameter rings. We only used data from plots with the control treatments of ambient CO_2, N, and temperature, as wells as nine or 16 species that represented the species richness commonly observed in old fields. C flux and pool measurements and estimation with BioCON data are described in Appendix S1: Section S1.1.

The impact of pocket gophers on C fluxes

The effect of pocket gopher disturbance on soil C pools was caused by a combination of gopher-induced changes
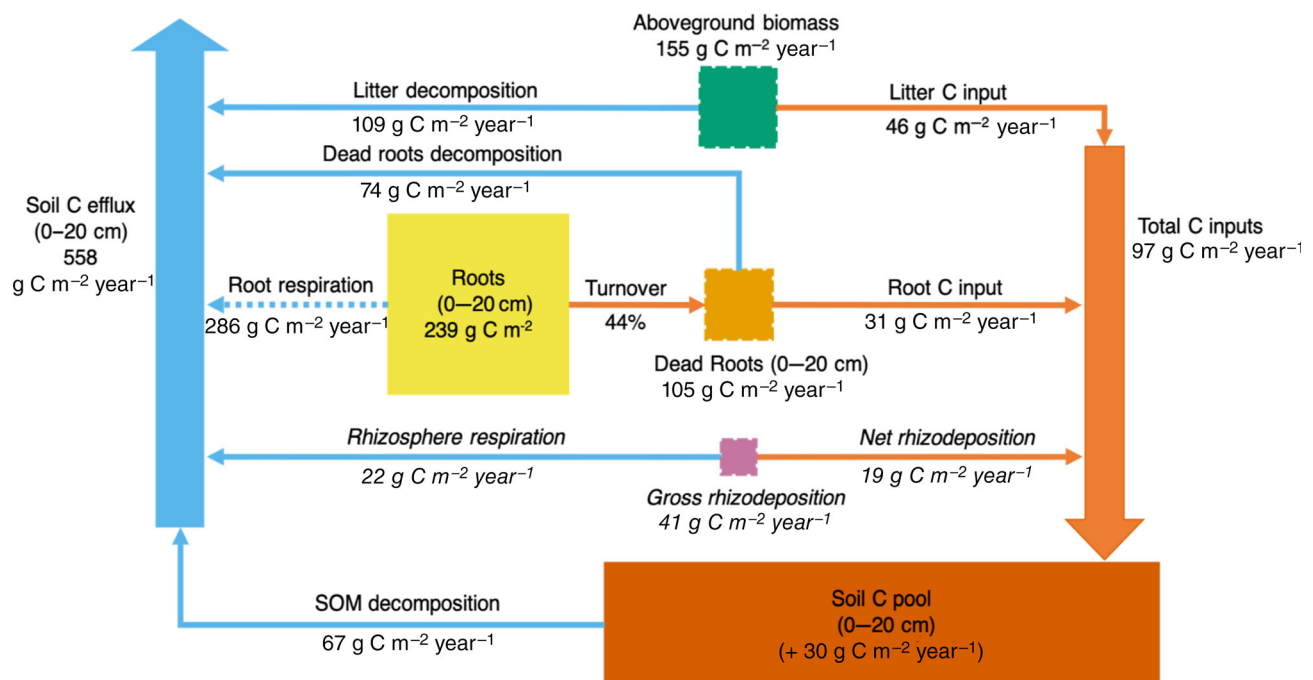

FIGURE 2 Average annual ecosystem C pools and fluxes at Cedar Creek Ecosystem Science Reserve (CCESR). The arrows represent C fluxes; the square blocks represent annual C inputs originating from vegetation, and the rectangle represents the total soil C pool at 0–20 cm depth. The square blocks with broken outlines represent annual gross primary production (GPP)

in the vegetation and in the SOM (Figure 1). We quantified these fluxes in order to parameterize the process model. We measured the intensity of soil disturbance caused by pocket gopher activities by recording gopher mound abundance, mound spatial distribution, and sizes, as well as identifying the gopher mound soil source. Furthermore, we also assessed the changes in NPP, and SOM decomposition rates induced by pocket gopher activities.

The intensity of gopher disturbance

In 2015, new gopher mound abundances were recorded in an area of 40 m × 79 m (between the first and fourth permanent transect) in all 21 old fields. A subset of seven old fields was selected that represented the different age groups and locations. GPS locations, diameters, and heights of gopher mounds produced in 2014, 2015, and 2016 were recorded in these seven fields with Trimble Geo 7× handheld data collector with a resolution of <50 cm. In the early spring (end of April) of 2015, before gophers actively produce mounds, mounds with little or no litter were recorded as produced in the fall of 2014. These gopher mounds were marked with flags. Gopher mounds that were produced in 2015 and 2016 were marked with flags with different colors from May to October of each year and recorded in the following spring.

Gopher tunnel depths, mound sizes, and mound soil weights were measured in the summer of 2015. Three mounds were selected randomly in five out of the above seven old fields, as no fresh gopher mounds were found in two fields in 2015. The soil was excavated near each mound to locate the tunnels, and the depths and tunnel diameters were recorded. Mound heights and diameters were measured, and the mound volumes were calculated, estimating the shape of mounds as paraboloids. The soil of each whole gopher mound was collected and weighed. The soil water content was measured to determine the mound soil dry weight.

Vegetation consumption

To quantify pocket gopher consumption of NPP per unit soil area, we first estimated the pocket gopher abundance in each field. We assumed that each pocket gopher produced 110 mounds annually (Seabloom & Reichman, 2001), then estimated their abundance based on the mound number. Pocket gopher plant consumption, and thereby the direct reduction in NPP, was estimated based on their abundance, average body weight (0.22 kg) (Tilman, 1983), daily feeding rate (119 g kg^{-1} day^{-1}; Gettinger, 1984), and the energy assimilation efficiency (54%; Gettinger, 1984).

We determined the NPP reduction due to mounds burying plants as follows. First, we estimated the parameters for a non-linear biomass growth model (monomolecular model) with biomass at the peak time and the length of the growing season (May to August). Assuming gopher mounds are produced at a constant rate over the growing season (Sparks & Andersen, 1988) and assuming no plants grow on the newly produced gopher mounds, the reduced biomass by mound burial can be calculated as the difference between the biomass at the peak time multiplied by the length of the growing season and the area under the biomass growth curve.

Aboveground biomass samples were collected in August 2017 on, and adjacent to, the gopher mounds that were created in 2014, 2015, 2016, and 2017, and in undisturbed areas (with no apparent old mounds) in each of the seven old fields. These four, year mounds formed chronosequences in vegetation re-establishment. We selected the 2017 mounds (0-year-old mounds) that were formed within 1 week before the biomass collection, therefore these mounds had no newly established plants present. Mounds in the previous 3 years were also all formed and marked in August, therefore the time interval between the different aged mounds was exactly 1 year. August is the peak biomass period at CCESR, with frost likely in September or early October, marking the end of the growing season. Therefore, resprouting from buried vegetation or seed germination on the selected mounds each year is minimal after August. During the biomass collection, we observed no resprouting of buried vegetation and all new vegetation originated from seed germination (Y. Yang, J. M. H. Knops, personal observations). Do note that mounds that we sampled in 2017 were formed in August. Mounds formed earlier in 2017, that we did not sample, could have some germinated plants, and along the edge of the mounds, some resprouted from buried vegetation. Therefore we may slightly underestimate the plant productivity in 2017. In each field, eight gopher mounds were randomly selected for each of the four age groups. For each mound, vegetation on the mound was collected in a quadrat that depended on the size of the mound, and the exact side length was recorded. Vegetation adjacent to the mound was collected in four 20 × 20 cm quadrats in four directions. In eight randomly selected areas with no apparent old mounds within each field, vegetation samples were collected in 50 × 50 cm quadrats. Samples were sorted to litter and live biomass, dried, and weighed.

In situ soil net N mineralization

In situ net N mineralization rates of gopher mound soil, the soil under mounds (0–20 cm), and soil in the

undisturbed area (0–20 cm) were determined in six of the seven fields during the 2016 growing season. Only six fields were examined because no new spring gopher mounds were found in one of the fields. In each field, four mounds and four locations in the undisturbed area were selected. In situ net N mineralization rates were measured twice: from late May to early July, and from early July to mid-August. At each mound, mound height was first measured (usually approximately 10–15 cm), then a PVC pipe (35 cm tall, 7.6 cm inner diameter) was inserted from the top of the mound until it reached 20 cm depth from the surrounding soil surface. The PVC pipe was loosely covered to allow gas exchange. Additional soil cores that corresponded to the same depths were collected adjacent to the PVC pipe to calculate the initial NH_4^+-N + NO_3^--N and total soil C and N. At the end of 5 weeks, soil samples were collected from PVC pipes and analyzed for final NH_4^+-N + NO_3^--N. A similar procedure was performed in the undisturbed area, except that the PVC pipes were inserted to 100 cm, where net mineralization rates in 20–60 cm and 60–100 cm depth intervals were measured. For soil NH_4^+-N + NO_3^--N analyses, we first extract NH_4^+-N + NO_3^--N from fresh soil with 1 mol KCl solution, then analyzed the extracted solution with a flow injection analyzer (Lachat Quickchem Flow Injection Analysis System, Lachat Instruments, Milwaukee, WI, USA).

Gopher disturbance model

A discrete-time process model was developed to simulate the effect of gopher disturbance on soil C pool changes at the ecosystem level (Figure 3 and Data S1: gopher_disturbance_model.R). The vegetation recovery time was first set in order to determine the number of stages of gopher mounds that existed in the simulated field. Taking 6 years of recovery time as an example, the field is undisturbed at year 1, and gophers form new mounds every year subsequently. A model assumption is that gophers avoid disturbed mound areas until the aboveground biomass is fully recovered after 6 years. With this assumption, after 6 years, there are seven distinct stages of gopher mound soil existing in the simulated field. The soil C pool (g m^{-2}) in the undisturbed area is modeled as the weighted mean of original undisturbed soil C pool (C_0) and C pool of old mounds soil (C_6) weighed by the fraction ($f_{i,t}$) of ground surface that each stage of mound soil covered:

$$C_{0,t} = \frac{(C_{0,t-1}) \times (f_{0,t-1} - f_{1,t}) + (C_{6,t-1}) \times (f_{6,t-1})}{f_{0,t-1} - f_{1,t} + f_{6,t-1}} + I_0 - k \times C_{0,t-1}.$$

(1)

In the equation, t is time (year); C_6 is assumed to become C_0 the next year, as the vegetation is mostly recovered on the gopher mounds, and gophers can come
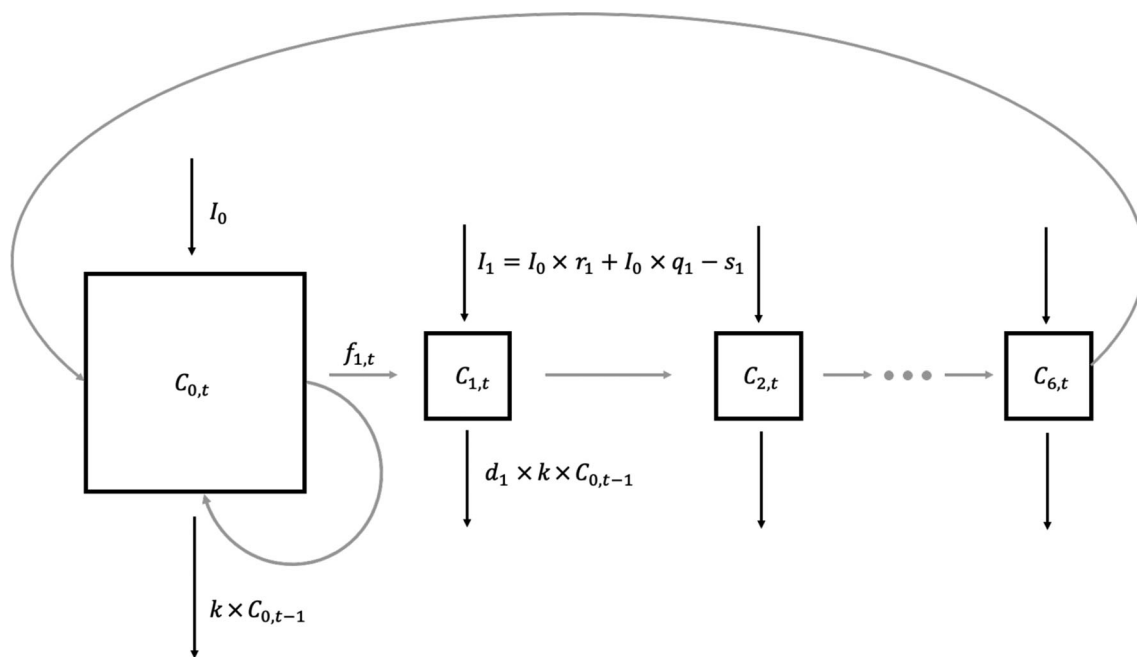

FIGURE 3 Graphic representation of the gopher disturbance model. At any given time (between years 7 and 200), seven soil stages are simulated in an old field: Undisturbed soil C_0, and soils covered by gopher mounds with different ages (C_1–C_6). The mean C pool of the old field is modeled as the mean of the C pool in the seven different stages of soils weighed by their fraction of the total area. Each stage of soil has its own unique fluxes of C input and output, and the fraction of each disturbed soil is determined by the area covered by 1-year-old mounds. The gray arrows represent the transition of different stages of soils, and the black arrows represent C fluxes

back to disturb again; $f_{1,t}$ is the proportion of ground surface that is covered by the newly created mounds at a given year; $f_{6,t}$ is the proportion of ground surface that is covered by the 6-year-old mounds at a given year; I_0 is the C input of undisturbed soil and all from vegetation C; k is the soil C decomposition fraction. Soil C pools of the area covered by mounds with age from 1 to 6 ($C_{i,t}$) were modeled as:

$$C_{i,t} = C_{i-1,t-1} + I_i - d_i \times k \times C_{i-1,t-1} \quad \text{for } i \in (1,6). \quad (2)$$

where $C_{i-1,t-1}$ is the C pool of gopher mounds soil in the previous year; I_i is the C input in the area covered gopher mounds with different ages, which is modeled as:

$$I_i = I_0 \times r_i + I_0 \times q_i - s_i \quad \text{for } i \in (1,6). \quad (3)$$

In the equation, I_0 is the total C input from vegetation when there is no gopher disturbance; $I_0 \times r_i$ calculates the total C inputs in areas covered by gopher mound of different ages; the total C inputs in gopher mound soil increases as the vegetation recovers, and r_i is the ratio of aboveground biomass on gopher mounds with different ages to that of the undisturbed area; the aboveground biomass on gopher mounds is acquired from the vegetation recovery curve (Figure 4b). Here we assumed root biomass recovers at the same speed as the aboveground biomass, because we found a significant correlation between aboveground productivity and root growth in the BioCON plots ($n = 486$, $p = 0.001$) (Appendix S1: Section S1.1). r_i is between 0 and 1. The C inputs from plants that were killed by gopher mounds were calculated with $I_0 \times q_i$. The amount of vegetation covered by the gopher mound increased as plants grow during the growing season. We modeled the C inputs from plants buried by gopher mounds with $I_0 \times q_i$, where q_i is the realized fraction of biomass at the time of burial. We assumed that the formation of new gopher mounds was constant during the vegetation growing season (late April to mid-August). The total amount of vegetation buried under gopher mounds of a specific growing season is the integral area under the vegetation growth curve. q_i is the quotient of the integral area under the vegetation growth curve divided by the product of the length of the growing season and peak amount of biomass in the undisturbed area (i.e., I_0). Litter burial by gopher mounds only happens in the first year, therefore $q_2 - q_6$ all equal 0. Biomass consumed by gophers is s_i. We assumed that gophers consumed vegetation in the disturbed area only in the first year, therefore $s_2 - s_6$ all equal 0. C decomposition was modeled as $d_i \times k \times C_{i-1,t-1}$, where d_i is the ratio of SOM decomposition in the disturbed area to undisturbed area. d_1 was based on the in situ N mineralization in the

disturbed and undisturbed area during the first year (Figure 4c–e). We assumed that the SOM decomposition rate in disturbed soil (gopher mounds) recovered to the undisturbed soil level (k) after the first year, therefore for $d_2 - d_6$ each equal 1.

The field-level soil C pool ($\overline{C}_t$) was calculated as the mean of soil pool of each stage of soil, and their proportion of ground surface coverage was:

$$\overline{C}_t = \sum_{i=0}^{6} f_{i,t} \times C_{i,t}. \quad (4)$$

All models had a time step of 1 year and ran for 200 years. All the parameters for the model are shown in Table 1.

With the gopher disturbance model, we simulated the soil C dynamics in the old fields under several levels of constant gopher disturbance (Figure 5a), natural grassland succession (Figure 5b), and prescribed burning (Figure 5c). The constant disturbance levels we chose were based on the disturbance level we found in CCESR and within the range of the highest level reported in previous publications (30%; Hobbs & Mooney, 1985). In the natural grassland succession scenario, we set the fraction of area covered by new gopher mounds each year ($f_{0,t}$) to vary based on the results in Figure 4a, with equation:

$$f_{1,t} = \frac{e^{\beta_{\text{age}} \times t + + \beta_{\text{intercept}}}}{1 + e^{\beta_{\text{age}} \times t + + \beta_{\text{intercept}}}}. \quad (5)$$

where β_{age} and $\beta_{\text{intercept}}$ are parameters of the zero-inflated beta regression model that we used to model the relationship between $f_{0,t}$ and field age. Half of the old fields at CCESR had been prescribed burned at a frequency of approximately every other year. We simulated the burning disturbance on top of grassland succession by removing aboveground litter every other year. We applied the Monte Carlo method to propagate errors for each of the above scenarios. The confidence intervals were constructed with simulations of 100,000 samples drawn from the means and the uncertainty ranges of the parameters reported in Figure 4 and the parameter represents gopher vegetation consumption (s_i). The s_i value was derived from the literature that did not report error terms, and we assumed a 30% uncertainty in the Monte Carlo simulations (Appendix S1: Table S1). In these simulations, we retained the parameters that were associated with climate factors such as annual C input from vegetation and SOM decomposition fraction, constant because we aimed to identify the particular impact of pocket gopher disturbance on soil C dynamics.
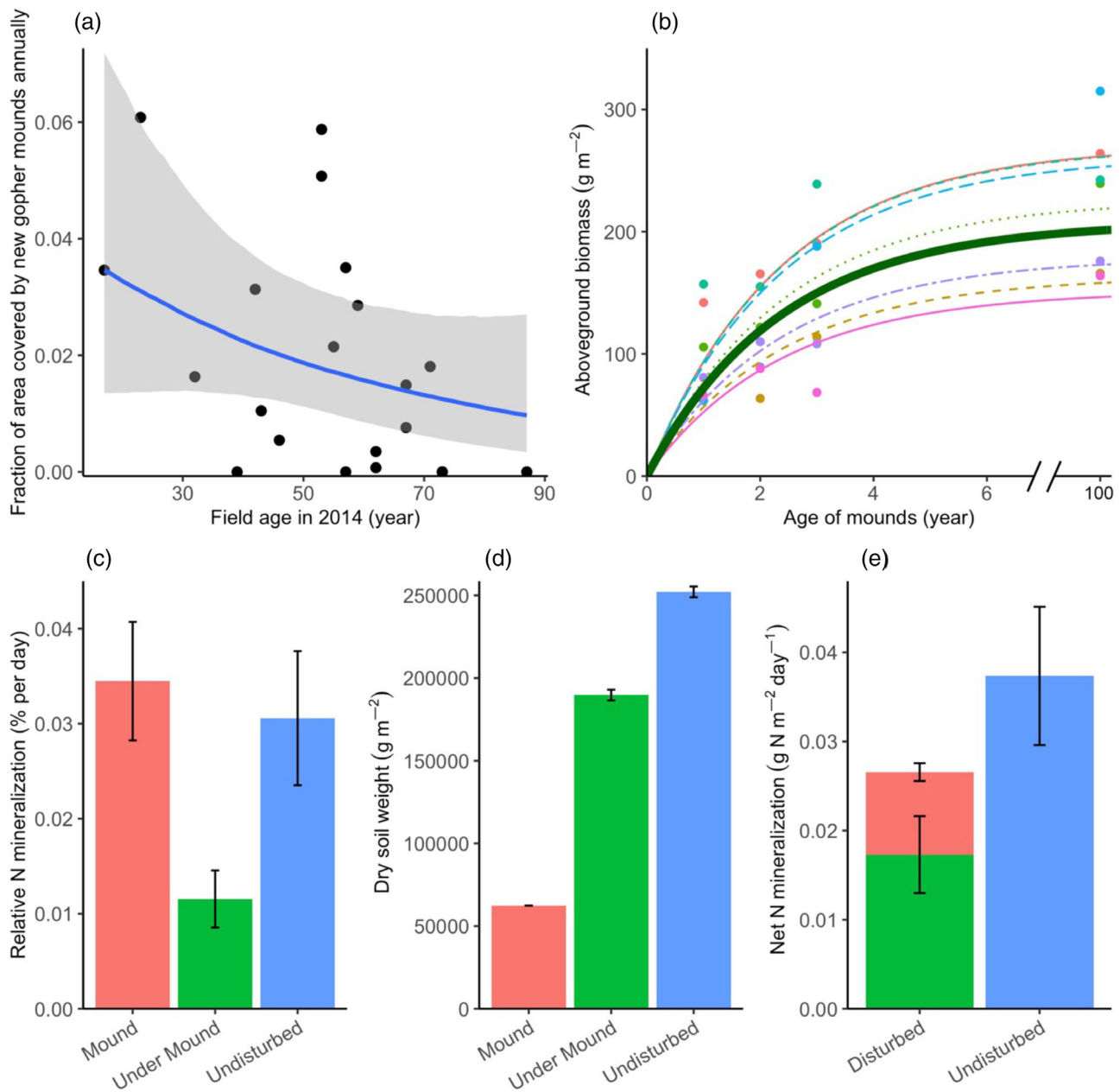
FIGURE 4 Pocket gopher influence in old fields at Cedar Creek Ecosystem Science Reserve (CCESR). (a) Gopher mound abundance changes after field abandonment. Dots represent the percentage of area covered by new gopher mounds annually, the blue line is the best fit of a Bayesian zero-inflated beta regression, and the gray area is the 95% CI. Note that the regression was only marginally significant (the 95% CI for the coefficient of field age is between −0.04 and 0.00). (b) Vegetation recolonization on the bare soil produced by gopher mounds. The best non-linear regression fit is monomolecular models. The dark green line represents the global fit for all fields, and the other lines represent six separate fields. (c–e) Soil N mineralization in gopher mound (red), under gopher mounds (green), and in undisturbed soil (blue). The data shown are the means ±1 SE. (c) Shows the relative N mineralization rate (% per day), which was calculated as net N mineralized in a day divided by soil total N content. (d) Shows the dry weights of the three types of soils in a 1 m^{-2} area. Mound soil and soil under mound together add up to the depth of 0–20 cm, and the depth of undisturbed soil is 0–20 cm. Note that the dry weight of mound soil is significantly lower compared with the other two types of soils. (e) Shows that total soil N mineralization (g N m^{-2} day^{-1}) in disturbed soil (gopher mound soil + soil under mounds) is significantly lower compared with undisturbed soil

Elasticity test

Gopher disturbance influences C inputs to the soil C pool by forming gaps and inhibiting vegetation growth, as well as increasing soil C losses by altering SOM decomposition. To evaluate how each of these processes influenced the overall gopher disturbance impact, we conducted elasticity tests on the model parameters. Each parameter

TABLE 1 Description of the gopher model parameters

Parameters	Unit	Definition and comments
$f_{i,t}$	% year^{-1}	Fraction of area covered by new gopher mounds each year, at age i and time t
$C_{0,t}$	g C m^{-2}	Soil C pool at 0–20 cm in the undisturbed area at a specific time
$C_{1,t} - C_{6,t}$	g C m^{-2}	Soil C pool at 0–20 cm area covered by first-year to sixth-year mounds at a specific time
$\overline{C}_t$	g C m^{-2}	Weighted mean soil C pool at 0–20 cm of both disturbed and undisturbed areas
I_0	g C m^{-2} year^{-1}	C input in the undisturbed area
$I_1 - I_6$	g C m^{-2} year^{-1}	C input in the area with first-year to sixth-year mounds
q_i	year^{-1}	The ratio of buried plant biomass to biomass in an undisturbed area. It was calculated as the quotient of the amount of biomass covered by gopher mounds divided by the undisturbed annual biomass in the unit area
s_i	g C m^{-2} year^{-1}	C in the biomass consumed by pocket gophers
k	year^{-1}	Soil C decomposition fraction in the undisturbed area
d_i	Dimensionless	A constant that controls soil C decomposition fraction in soil covered by first-year to sixth-year gopher mounds
r_i	Dimensionless	The ratio of biomass on gopher mounds (first year to the sixth year) to that of undisturbed area. Biomass on gopher mounds of different ages was calculated using a vegetation recovery curve

was set to vary, while other parameters were kept constant. A reference scenario was first selected based on empirical measurements and the estimated ecosystem C budget. Each parameter was set to 50% and 200% of their reference value in the test scenarios.

Data analysis

The area of soil surface that was covered by gopher mounds was determined by first mapping the recorded coordinates of gopher mounds, then expanding a circular buffer from each mound center point with the measured diameter and summing these areas together. We calculated the overlap between gopher mounds that were created in two consecutive years. Bayesian non-linear hierarchical models were used to estimate the gopher mound aboveground biomass recovery time. We assumed that the aboveground biomass in the undisturbed area was the asymptote of the growth curve. As the modeling requested the field age to be numeric, we set the field age for the undisturbed soil to 100. Non-linear functions that were used to fit the data included the piecewise model, Michaelis–Menten model, and monomolecular model, which are commonly used to model plant growth. Leave-one-out cross-validation (Vehtari et al., 2017) was applied for model selection. The best-fit model was the monomolecular model using the same recovering time for all fields, but with different maximum recovered biomass levels for each field. The relationship between the fraction of area covered by the new gopher mound annually and

field age was modeled with a zero-inflated beta regression. The N mineralization rates of gopher mounds, the soil under gopher mounds, and soil in the undisturbed area were calculated based on the N mineralization rates and dry soil weight per unit area at different depths. The dry mound soil weights per unit area were estimated by constructing the linear relationship between dry mound soil weights and areas covered by gopher mounds. The statistical significance of soil N content and mineralization rates was tested with a nested ANOVA.

All statistical analyses were performed using R version 3.5.2 (R Core Team, 2018). The *tidyverse* package (Wickham, 2017) was used to import data and transform data sets; *lme4* (Douglas et al., 2015) was used to perform nested ANOVA; *sp* (Roger et al., 2013), *raster* (Hijmans, 2019), *rgdal* (Bivand et al., 2019), *rgeos* (Bivand & Rundel, 2018), *leaflet* (Cheng et al., 2018), *maps* (Becker, Brownrigg, Minka, et al., 2018) and *mapdata* (Becker, Brownrigg, Wilks, 2018) were used to analyze gopher mound spatial distribution; *rstan* (Stan Development Team, 2019) and *brms* (Bürkner, 2017) were used to perform Bayesian analyses; *ggplot2* (Wickham, 2016) was used to construct the figures.

RESULTS

Gopher mounds

Gopher mounds are typically circular areas with a mean diameter of 43.5 ± 0.3 cm ($n = 4368$). We found no
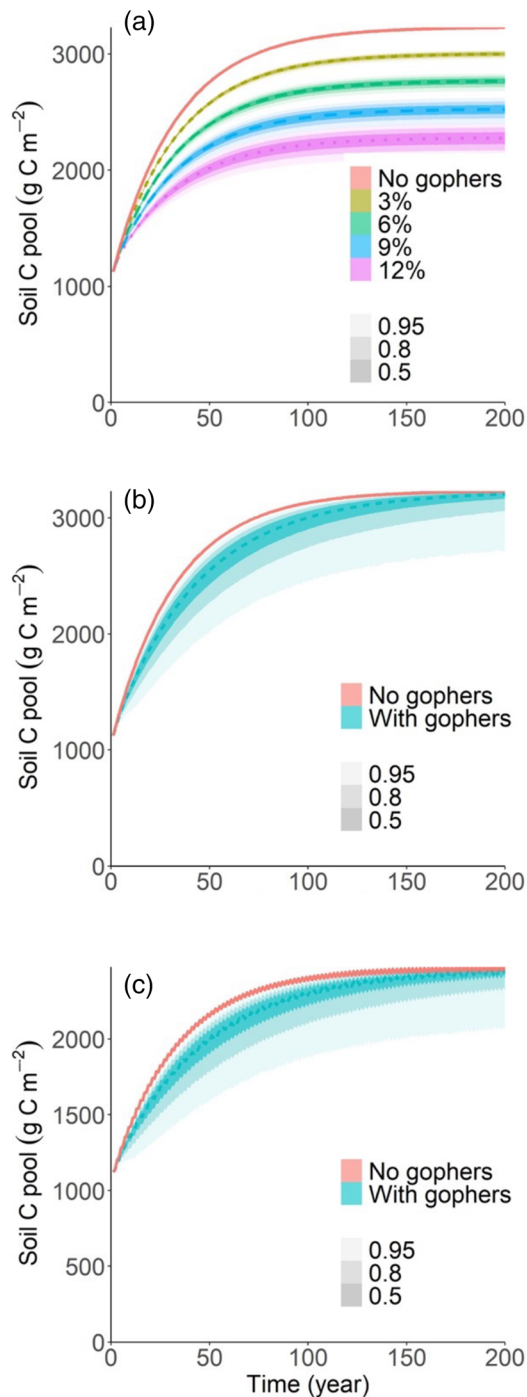
significant pattern in mound sizes with field abandonment age or among the three sampling years. Among the 21 old fields, there was no significant difference in gopher mounds abundance between the burned and unburned half of each old field controlling field age ($n = 21$, $p = 0.23$, two-way nest ANOVA) (Appendix S1: Figure S11). Therefore, we combined gopher mound abundance in both burned and unburned areas when considering gopher disturbance levels in each field. Total gopher mound abundance decreased with old field abandonment age, with gopher mounds being absent only in some of the older fields and totaling up to 1734 ha^{-1} in recently abandoned fields. This range in gopher mound abundance corresponded to 0% to 6% annually disturbed soil area (Figure 4a). This decreasing trend is marginally significant (Bayesian zero-inflated beta regression, the 95% CI for the coefficient of field age is between -0.04 and 0.00), and gopher mound abundance in the mid-age old fields (30–70 years) varied between 0% and 5.8%. In the seven old fields where we recorded the gopher mound locations and sizes for 3 years, new gopher mounds formed near older ones each year, yet only 3.5% of the new mounds overlapped with older mounds. In other words, each year, 96.5% of newly formed gopher mounds covered new soil areas. Foraging tunnels were at 22.2 ± 1.2 ($n = 15$) cm depth, with a mean tunnel diameter of 7.4 ± 0.2 cm ($n = 15$). Foraging tunnels contributed 76%, and access tunnels contributed 24% of the soil in the gopher mounds. Therefore, most of the gopher mound soil originated from the surface soil or from 20 cm deep. This was consistent with the gopher mound soil total N, which did not differ from the undisturbed soil at 0–20 cm ($n = 24$, $p = 0.95$, Tukey's post hoc test), but was higher compared with deeper depths ($n = 24$, $p < 0.0001$, Tukey's post hoc test) (Appendix S1: Figure S10). Therefore, pocket gophers at CCESR disturbed 0%–6% of the soil in old fields annually, and this disturbance mostly focused on the surface soil. Therefore, redistribution of deeper subsurface soil was minor and largely insignificant.

Vegetation recovery on mounds

Gopher mounds formation significantly reduced aboveground vegetation biomass. Biomass next to these newly formed gopher mounds did not significantly differ from the undisturbed areas. The level of aboveground biomass on gopher mounds and the undisturbed areas did vary among fields; however, the biomass recovery rates on gopher mounds followed the same recovery pattern (Figure 4b). Compared with the undisturbed area, on average, 44% of aboveground biomass on gopher mounds

FIGURE 5 Modeled old field soil C pool after agricultural land abandonment with gopher-induced soil disturbance. Shown are (a) fixed gopher abundance over successional time (0%, 3%, 6%, 9%, and 12% indicate the percentage area covered by new gopher mounds annually), (b) with the observed gopher abundance decrease over successional time (see Figure 4a for the observed gopher abundance in relation to field abandonment age), and (c) with the observed gopher abundance decrease over vegetation succession and frequent prescribed fire (every other year). Red lines and shades are the simulations of C dynamics in the undisturbed areas, whereas other color lines and shades are the simulations of the gopher disturbed areas. The confidence intervals were constructed with the Monte Carlo simulations. The different shades represent 50%, 80%, and 95% confidence intervals

recovered after 1 year, 46% recovered after 2 years, and 60% recovered after 3 years. The fitted growth model estimated that 6 years are required to recover 95% of the aboveground biomass of the undisturbed areas.

Gopher mound soil N mineralization

In situ N mineralization rates in gopher mound soil, the soil under gopher mounds, and the undisturbed soil were measured twice in 2016, in spring and summer. We found no significant difference between the two sampling times (nested two-way ANOVA, $F_{[1,69]} = 0.81$, $p = 0.371$), nor any interaction between measuring time and soil type (nested two-way ANOVA, $F_{[2,69]} = 2.06$, $p = 0.135$). Therefore, we used the average relative N mineralization rates of the two measurements for the different soils, which were calculated as net N mineralized in a day divided by soil total N content. Nested one-way ANOVA ($F_{[2,22]} = 5.34$, $p = 0.018$) showed that there was no significant difference between the relative N mineralization rates in the gopher mound soil and the undisturbed soil ($p = 0.863$, Tukey's post hoc test). However, the soil under mounds did have significantly lower relative N mineralization rates compared with both the gopher mound soil and the undisturbed soil ($p = 0.015$ and $p = 0.047$ respectively, Tukey's post hoc test) (Figure 4c). Gopher mounds contained on average 6.2 kg dry soil m^{-2} (Figure 4d), which is equivalent to the weight of 33% of soil under gopher mounds (0–20 cm depth). Assuming gopher mound soil originates largely from the 0–20 cm depth of soil, the disturbed areas, which consist of gopher mound soil and soil under gopher mounds, have 30% lower N mineralization than the undisturbed areas. This reduced N mineralization is caused by the decrease in soil N mineralization under the gopher mounds (Figure 4e). We then used the N mineralization rates to estimate C mineralization rates. The annual N mineralization was approximately 3.6% N year^{-1} calculated by multiplying weighted daily relative N mineralization (0.017% N day^{-1}; Figure 4c,d) with the number of frost-free days at CCERS (210, April to October). This was comparable with the annual C mineralization rate, which was approximately 3.4% C year^{-1} calculated from the ecosystem C budget (Figure 2). Therefore, we can assume that the C:N ratio remained constant during SOM decomposition and soil C mineralization could reduce by 30% in disturbed soil.

Long-term soil C pool

We parameterized a process model with the short-term field measurements at CCESR to simulate the long-term

effect of pocket gopher disturbance on the soil C pool. Consistent with results from previous research (Knops & Bradley, 2009), we found that the soil C pool accumulated asymptotically in old fields without gopher disturbance (Figure 5a). In fields with pocket gopher disturbance, the soil C pool also accumulated, following saturated curves. However, pocket gopher soil disturbance reduced C accumulation rate and the equilibrium of the soil C pool, and the asymptote decreased with increasing gopher abundance (Figure 5a). With the observed pocket gopher disturbance intensity at CCESR (up to 6% annually disturbed area), the equilibrium C pool was reduced by up to 13% at 100 years after field abandonment, which was equivalent to 15.25 Mg CO$_2$ ha^{-1}. Such C dynamics were simulations with constant gopher disturbance and vegetation productivity. In fact, in the old fields at CCESR, the intensity of gopher disturbance did decrease with field age (Figure 4a). We assumed that gopher disturbance followed a similar trend between the burned and unburned areas because there was no significant difference in mound abundance. This is not surprising, because both areas are next to each other and comprise one field unit. When incorporating the gopher decreasing activity into the process-based model, the effect of disturbance on soil C pool became transient and diminished over time in both burned (Figure 5c) and unburned areas (Figure 5b). The large variability of the C dynamics under gopher disturbance is mainly due to the uncertainty of the relationship between gopher abundance and field age (Figure 4a). In the unburned areas, gopher disturbance during early succession reduced the soil C accumulation rates and, at year 50, the soil C pool in fields was 6% lower compared with fields with the absence of pocket gophers. The recovery of the soil C pool to the pre-agriculture levels in fields with pocket gopher activities required 40 years longer compared with the undisturbed fields. With the prescribed burning, the pattern of pocket gopher disturbance impact on soil C dynamics was essentially the same as in the unburned scenario. However, prescribed burning led to a 24% lower long-term soil C pool equilibrium, because fire removes aboveground litter. Combining these results demonstrated that pocket gopher soil disturbance could significantly reduce both the soil C pool equilibrium and the C accumulation rate after field abandonment. However, compared with pockets gophers, fire had a much larger impact on old field soil C dynamics.

Elasticity analysis

Pocket gophers influenced the soil C pool equilibrium and rate of change after field abandonment because the

gophers reduced soil C inputs by consuming plants, burying the vegetation by their mounds, and affecting the time that was required for vegetation to re-establish on the gopher mounds. Pocket gopher soil disturbance also changed the rate of soil C losses, due to changes in SOM decomposition. We conducted elasticity analyses for the parameters that represented each of the above processes to test their relative importance. For all elasticity analyses, we set the annually disturbed soil area to 3% and assumed gopher activities did not change over time after field abandonment. We found that the most important factor influencing the impact that pocket gophers had on soil C was the decrease in C inputs, especially the time that was required for the vegetation to recolonize on gopher mounds. Doubling the recovery time from 6 years to 12 years decreased the soil C pool level by 12% (Appendix S1: Figure S1). The two remaining processes that influenced C inputs, plant consumption and vegetation buried by gopher mounds, had negligible effects on the model outcome (Appendix S1: Figures S3 and S4). The increase in the soil C decomposition rate of disturbed soil reduced the soil C pool equilibrium by 2% when doubled, making this effect size much smaller than that of vegetation recovery time (Appendix S1: Figure S2). Therefore, the reduced C inputs caused by the time that was required for the vegetation to recolonize gopher mounds was the key factor that determined most of the impact that gophers had on the soil C pool.

In addition to the parameters that represented the impact of pocket gophers on soil C inputs and outputs, the outcome of the process model was also influenced by parameters that were not directly linked to pocket gopher activities, such as the rate of soil C decomposition fraction, vegetation C input rate in the undisturbed soil, and the initial soil C pool. These parameters are controlled by environmental factors such as temperature, precipitation, and soil texture, as well as the soil C condition after agricultural abandonment. Performing elasticity analyses on those parameters can help to determine if the impact of pocket gophers on the soil C pool interact with environmental factors. We found that changing the decomposition fraction and C input from the vegetation of the undisturbed soil strongly impacted the soil C equilibrium of fields with or without pocket gopher disturbance (Appendix S1: Figures S5 and S6). However, the relative impact of pocket gophers on soil C compared with the undisturbed fields remained constant. Furthermore, the initial C pool size only impacted the time for the soil C pool to reach the equilibrium level and had only a small impact on either the soil C equilibrium level or the effect of gopher disturbance (Appendix S1: Figure S7). Therefore, the equilibrium of the soil C pool was largely determined by environmental conditions that determined C inputs and losses, and the impact of pocket gophers on soil C pool was independent of the environmental factors and the initial state of soil C in old fields when assuming that the disturbance intensity was constant.

DISCUSSION

Using a process model, we found that in the long-term, pocket gopher disturbance reduced the soil C accumulation rate and decreased the C pool equilibrium level in old fields. Furthermore, the influence of pocket gophers on soil C pools diminished during the grassland stage of old field succession, as the abundance of pocket gophers decreased with abandonment age in the old fields. Another goal of the process model was to determine the relative importance of processes that linked gopher activities to the soil C pool. The elasticity analyses of the process model demonstrated that the vegetation recolonization of gopher mounds is the key factor that determines the impact of gophers on the soil C pool. These results suggest that managing pocket gopher population sizes or accelerating vegetation recolonization on gopher mounds can minimize the negative impact of pocket gophers on soil C sequestration in old fields.

Gopher disturbance and primary production

Pocket gopher activities reduced NPP, and the slow vegetation recolonization on gopher mounds is the primary mechanism causing this reduction in C input. In contrast, pocket gopher directly consume vegetation as food, and the impact of the gopher mound by burying vegetation has only a minor impact. The slow vegetation recolonization on gopher mounds can be attributed to the high mortality of seedlings caused by high herbivory risk and dry soil conditions (Davis et al., 1995; Reichman & Seabloom, 2002). Previous research (Reichman et al., 1993) has demonstrated that gopher mounds enhance plant growth around mounds (within 10 cm distance), which is likely to be due to the accelerated nutrient turnover of buried litter (Clark et al., 2018). However, in this study, we did not find any significance in biomass within 20 cm of gopher mounds compared with the areas undisturbed at the end of the growing season. The increased available nutrients on gopher mounds are either transient or leached to deeper soil depths in these sandy soils and did not impact the NPP over the entire growing season.

Gopher disturbance interactions with vegetation composition

The effect of gopher disturbance on the soil C pool is controlled by gopher abundance, which is mainly influenced by the vegetation composition of their food source (Seabloom & Reichman, 2001). The foraging behavior of gophers depends on the distribution of their food resources (Seabloom & Reichman, 2001), and pocket gophers prefer early successional species rather than late-successional species (Behrend & Tester, 1988). Such a foraging preference can explain the decrease in gopher activities with field age in old fields observed by this study and by Inouye et al. (1987b). Gopher disturbance also influenced the composition of the vegetation. The old fields at CCESR were not actively managed after agricultural abandonment, and the dominant vegetation slowly transitioned from annual species to perennial C3 grasses, then to perennial C4 grasses (Clark et al., 2019; Tilman, 1994). The vegetation on gopher mounds primarily consisted of early successional annual forbs and grasses (Huntly & Inouye, 1988), therefore gopher activities could slow the progression of vegetation succession (Huntly & Inouye, 1988), and prolonging the period that gophers are abundant after land abandonment. The late-successional C4 grasses are competitively superior and eventually replace early successional plant species; however, these C4 grasses have slow colonization rates, limiting their spread within CCESR. This may explain the observed high variability of gopher mound abundance in some of the mid-to old-age fields at CCESR and the large uncertainty range of C dynamics under gopher disturbance and natural succession.

Mechanisms of how gopher disturbance reduces the soil C pool

Our study indicated that the decrease in soil C accumulation in old fields is caused by a long-term reduction of C input on gopher mounds, which differs from mechanisms raised in previous studies. The mechanisms by which burrowing mammals decrease soil C and nutrient pools can be summarized into three parts: increased SOM decomposition in gopher mounds (Canals et al., 2003; Litaor et al., 1996), redistribution of deeper soil with low C content to the surface soil horizon (Inouye et al., 1987b; Litaor et al., 1996), and root biomass consumption (Sherrod & Seastedt, 2001). Putting our study in perspective, first, we did not find a significant difference in N mineralization between mound soil and undisturbed soil. Gopher mound soil has a lower bulk density than undisturbed soil, therefore it may have improved aeration and microbial activity. However, the soil at CCESR is extremely sandy (Grigal et al., 1974) and soil at the surface rapidly dries out. The potential enhanced microbial activity in gopher mound soil by increase aeration may not be realized due to the lack of moisture. Unexpectedly, we did find that the soil under gopher mounds had significantly lower N mineralization compared with the undisturbed soil, which may be caused by reduced aeration and lower soil temperature once it was covered by gopher mounds. Second, we did not find the C and N content in gopher mound soil to be significantly lower than in undisturbed soil when compared within each field. This result contrasts with research by Inouye et al. (1987b), who found that gopher mound soil had lower N content compared with soil without gopher mounds. The discrepancy between the two studies is likely to be because Inouye et al. (1987b) compared the N content in gopher mound soil to undisturbed soil at 0–10 cm, whereas we did the comparison to undisturbed soil at 0–20 cm, as we found that the gopher mound soil was mostly taken from these depths at CCESR. The difference in N content between gopher mound soil and undisturbed soil at 0–10 cm was small, although statistically significant, and may disappear once mixed in with soil from 10–20 cm. Lastly, although we did not directly measure the root consumption by gophers, we did estimate gopher NPP consumption based on published daily consumption and assimilation rates (Gettinger, 1984) and incorporated this in the process model. The elasticity test of the model showed that the change in the NPP consumption of pocket gophers had little effect (Appendix S1: Figure S3), suggesting root consumption by gophers had only a limited influence. Note that previous research was largely based on short-term soil chemistry surveys that compared C and nutrients in gopher mound soil and undisturbed soil, whereas this study incorporated the main processes affected by gopher activities with an ecosystem C budget and made predictions on the long-term soil C pool change.

Gopher disturbance effect in relation to longer-term old field succession and prescribed burning

The long-term trend of soil C pool under gopher disturbance that was demonstrated by our model (Figure 5b) can be altered in the unburned half of each old field when these areas are invaded by woody species. First, gopher activities would have had less impact on the productivity of woody species, because gopher mounds cannot bury adult trees and tree seedlings are more likely to resprout when buried. Second, tree invasion can lead to

the redistribution of ecosystem C from soil to plant biomass. Laungani and Knops (2009) found that at CCESR the growth of tree species (*Pinus strobus* and *Quercus ellipsoidalis*) led to a decrease in soil C and an increase in aboveground biomass C (*P. strobus*) or belowground biomass C (*Q. ellipsoidalis*). However, the timeline of grasslands transitioning to savannah or forests at CCESR is uncertain. Tree invasion in CCESR old fields is at a slower rate compared with the northeastern USA, which could be attributed to poor soil nutrients, herbivory, and slow growth rates (Inouye et al., 1994). Currently, only three out of the 21 old fields are invaded by tree species, one by *P. strobus* and two by *Populus tremuloides*. With climate change and rising atmospheric CO_2, tree invasion in the old fields may be accelerated in the future, therefore reducing the impact of gopher disturbance on soil C.

In contrast, in the burned half of each old field, prescribed burning prevents the encroachment of woody species and delays the succession from grasslands to forests. Yet fire can still interact with the impact of gopher disturbance on old field soil C. Burning impacts the vegetation composition by removing fire-intolerant species and changing competitive interactions among species, which in turn affect gopher abundance. In some grasslands, such as the Konza prairie (Gibson & Hulbert, 1987), frequently prescribed burning leads to increased dominance of C4 grasses, because burning is usually done in early spring, which negatively impacts cool-season species such as C3 grasses and some forbs. However, several long-term studies at CCESR found that prescribed burning had no impact on functional group composition in the old fields (Knops, 2006; Li et al., 2013) which explains that no significant difference was found in gopher mound abundance between the burned and unburned half of the old fields (Appendix S1: Figure S11). The minimal impact of fire on old field vegetation composition at CCESR was attributed to the infertile soil and low primary production (Knops, 2006) compared with more productive grasslands. Overall, in productive grasslands, prescribed fire can promote the dominance of C4 grasses and therefore is likely to accelerate the decline of gopher abundance over the long term. We acknowledge the simulations of old field soil C dynamics presented in this study include little interaction between fire and gopher abundance, which may better represent old fields with infertile soil and low primary productivity.

Gopher disturbance in relation to other factors that affect old field C pool

Total C input from NPP and SOM decomposition strongly impacts the soil C accumulation rate and determines the equilibrium soil C pool (Appendix S1: Figures S5 and S6). The elasticity analysis of the process model showed that the effect of gopher disturbance on old field soil C accumulation had little connection with the change in soil C input and output. This suggests that gopher disturbance acts as an additive effect on top of environmental factors such as climate, herbivory, soil texture, and soil moisture. Do note that several other environmental factors may have potential complex interactions with gophers. For instance, the relative abundance of C4, compared with C3 grasses increased soil C accumulation (Knops & Bradley, 2009; Knops & Tilman, 2000; O'Brien et al., 2010; Spiesman et al., 2017), which can be attributed to the higher productivity and lower decomposition rates of C4 grasses (Zuo & Knops, 2018). Pocket gophers preferentially consume C3 grasses (Behrend & Tester, 1988; Seabloom & Reichman, 2001). Therefore, in C3 grass-dominated old fields, increased pocket gopher abundance can further enhance the decreased soil C accumulation associated with increased C3 grass abundance, whereas with higher C4 grass abundance, the associated lower pocket gopher abundance may further enhance soil C accumulation. Gopher-induced soil disturbance can also potentially impact other soil properties such as erosion, soil compaction, and creating shelters for other animals (Huntly & Inouye, 1988; Reichman & Seabloom, 2002; Sherrod et al., 2005; Yurkewycz et al., 2014). However, we had no indication that any of these soil factors interacted with or changed the pocket gopher impact.

Gopher disturbance model limitations

The gopher disturbance model that we constructed here can identify the mechanisms by which gopher activities influence C dynamics. However, like any model, it has its limitations. First, the model does not explicitly model the feedback between soil N and C because the interaction between N addition and gopher disturbance can be complicated. Increased soil N, from N deposition, for instance, can promote soil C accumulation (Knops & Bradley, 2009), especially at CCESR because N limits plant productivity (Tilman, 1984). However, increased N also increases C3 grass dominance (Wedin & Tilman, 1996), which can lead to higher pocket gopher abundance and therefore further decrease the soil C pool. To capture the interaction between N addition and gopher disturbance further data from controlled experiments are needed. In addition, greater N mineralization can also support an increase in vegetation productivity, however, we did not find any enhanced vegetation growth near gopher mounds in this study. For regions where biomass is increased around gopher mounds,

additional C input needs to be accounted for when parameterizing the gopher disturbance model. Second, to parameterize the soil organic C decomposition, we used soil N mineralization to estimate soil C mineralization, because in situ soil mineral N accumulation is much easier to measure than gaseous CO_2 emissions. The annual soil N mineralization rates and C mineralization rates are comparable at CCESR (as described in the Results section), supporting the use of soil mineral N increases as a proxy for soil C mineralization. In addition, the elasticity analyses indicated that changes in the decomposition rates only induced a marginal impact on the soil C dynamics. Therefore, any error induced by using soil mineral N as a proxy for soil C mineralization should have minimal impact on the modeling results. Nevertheless, use of a constant C:N ratio during SOM decomposition was not necessarily valid at other locations. Measuring in situ C and N mineralization rates simultaneously across the growing season would be preferred to accurately obtain the parameter values. Third, the soil C inputs on gopher mounds were parameterized based on biomass data collected on mounds established at the standing biomass peak in August. We did not include any new biomass accumulated on mounds established earlier in the growing season. This approach may underestimate the C input on the gopher mound. However, such underestimation should be minimal, because we observed that vegetation re-establishment on new mounds was scarce. In addition, we also used a fixed ratio between the aboveground and belowground biomass when considering the vegetation C input. This assumption is valid for the re-establishment of perennial species, as we found that there was a significant correlation between aboveground and belowground NPP in BioCON plots with only perennial species. However, this may not be the case for new seedlings. Therefore, additional data on the linkage of aboveground and belowground biomass growth of new seedlings on gopher mounds are needed to improve the model parameterization. Lastly, we aimed to identify the effect of gopher disturbance, and all simulations used constant climate factors, which allowed us to determine the soil C equilibrium. However, future climate change may disrupt such equilibrium, because the increasing temperature can promote vegetation productivity, as well as SOM decomposition. Nonetheless, the extent of climate change impact on the C inputs and outputs is highly uncertain, especially considering the increasing frequency of severe climate events such as drought and storms. Sophisticated ecosystem models, such as DayCent (Del Grosso et al., 2000, 2010; Parton et al., 1998), can incorporate the gopher disturbance model developed here, to further increase their precision in predicting future old field C dynamics.

Burrowing mammals and soil C

Previous studies on the impact of burrowing mammals on soil C have mostly focused on comparing current C pool and fluxes between disturbed and the undisturbed areas such as vegetation biomass (Jones et al., 2008; Sherrod et al., 2005), SOM decomposition (Yurkewycz et al., 2014), and soil efflux (Clark et al., 2016). However, the long-term impact on soil C dynamics has not been examined, because of the slow accumulation rates of soil C and the requirement for intensive soil sampling due to the heterogeneity of disturbed soil. Our approach of using a simulation model allowed us to examine the impact of pocket gophers on soil C. In addition, our process model also can be used to examine the impact of other burrowing mammals. While the depth of the pocket gopher soil disturbance simulation was mostly set at 0–20 cm, we also simulated the scenario in which the mound soil originated below 20 cm and investigated how soil C changed at the 0–40 cm depth (Appendix S1: Figures S8 and S9). We found that such a soil disturbance can lead to an increased total soil C pool in the soil profile. Therefore, whether soil disturbance caused by burrowing mammals leads to soil C loss depends on the soil depth at which they are most active. Mound-building fossorial mammals, such as zokors (Spalacidae), African mole-rats (Bathyergidae), and bamboo rats (Rhizomyinae) have not been as well studied as North American pocket gophers, but they share similar root foraging behavior and tend to excavate tunnels at 10–30 cm depth and create mounds on the soil surface (Gabet et al., 2003). Therefore, these mammals are likely to have similar effects in terms of soil disturbance and soil C pool as do pocket gophers. In contrast, semifossorial mammals, such as prairie dogs (Sciuridae) and plains vizcacha (Chinchillidae), consume aboveground vegetation and excavate tunnels at much deeper depths (>30 cm) only for food caches and dens (Van Vuren & Ordeñana, 2012). Over time, the semifossorial mammals redistribute surface soil to a deeper depth and therefore may increase soil C sequestration (Schiedung et al., 2019). However, whether such soil redistribution is significant enough to affect the ecosystem C storage also depends on the population dynamics of the burrowing mammals and the disturbance effect on vegetation growth. Therefore, quantitative studies linking animal ecology, population dynamics, and vegetation growth with soil C pool change are needed to determine the long-term effects of different burrowing mammals on the ecosystem C pool.

CONCLUSIONS

This study examined the impact of gopher disturbance on soil C accumulation after agricultural abandonment. We

demonstrate that pocket gopher disturbance slowed down old field soil C sequestration, primarily because the mound building by gophers created vegetation gaps, reducing plant primary production and therefore reducing C inputs into the soil. At CCESR, gopher abundance decreased with field abandoned age, which is likely to be caused by the decrease in gopher preferred food sources as succession changes the vegetation composition. Therefore, gopher disturbance's impact on soil C is transient and decreases over time. This indicates that gopher population dynamics alongside vegetation successional gradients are key in determining gopher impact on soil C. We also demonstrated that the depth from which burrowing mammals redistribute soil to the surface is a key factor in determining the overall mammal impact on soil C dynamics. Simulations of our process model show that fossorial mammals, such as pocket gophers, that maintain burrows at near-surface depth have a negative impact on soil C sequestration and soil C pools. In contrast, semifossorial mammals, such as prairie dogs, that excavate tunnels at much deeper depths can increase soil C accumulation due to their mixing of soil horizons. Overall, environmental factors, such as climate, soil texture, and prescribed burning, have the greatest control on the C sequestration in old fields. However, as we show in this study, pocket gopher disturbance can be a significant factor that reduces the rate of soil C accumulation in old fields.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the EDI Data Portal as follows: Aboveground biomass on and around gopher mounds (Yang, 2021a), https://doi.org/10.6073/pasta/18390a7d0adbec9aa7d1e01efeccfd76; Soil N mineralization in gopher mounds and soil under gopher mounds (Yang, 2021c), https://doi.org/10.6073/pasta/265f32b8acc6e5ff0fde44e98467462e; Gopher mounds coordinates (Yang, 2021b), https://doi.org/10.6073/pasta/42ed34a9d6af521c83fc1655349177b3;

BioCON soil C flux (Reich, 2020b), https://doi.org/10.6073/pasta/b1dd62216ee0b281b8109f3081e455f3; BioCON soil C (Reich, 2021e), https://doi.org/10.6073/pasta/bef34a71f50629a2a1ea4ee5f7c63ded; BioCON aboveground biomass (Reich, 2021b), https://doi.org/10.6073/pasta/20d6633c64a977f889cfbe6d2e7a6b84; BioCON aboveground biomass C and N (Reich, 2021a), https://doi.org/10.6073/pasta/0115c585f9eef4a3fd1748ad49814b82; BioCON root biomass (Reich, 2021c), https://doi.org/10.6073/pasta/c3eaf35e30fc5ccbec4cae48192ea7b3; BioCON root C and N (Reich, 2021d), https://doi.org/10.6073/pasta/e4b0ab9dfa9e0fda4440f4e9a1ee1d62; BioCON root ingrowth (Reich, 2020a), https://doi.org/10.6073/pasta/d307637c4582713659a27cbd209a1d78. Code for the gopher disturbance model (Yang & Brassil, 2021) is available on Zenodo: https://doi.org/10.5281/zenodo.5555258.

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