A cellular automaton model for grasshopper population dynamics in Inner Mongolia steppe habitats

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ABSTRACT

We developed a cellular automaton model for the spatiotemporal dynamics of grasshopper (*Oedaleus decorus asiaticus*) populations with a density of 3–12 ind m^{-2} in a typical semiarid steppe. The model simulates grasshopper dynamics within each cell and dispersal between adjacent cells at each time step from the completion of hatching to ovipositing. After the model parameters were obtained or calibrated, the natural growth of grasses (the preferred food of *O. d. asiaticus*), and their variation after being fed on by cattle and grasshoppers, were modeled to explore grasshopper–plant interactions. Dispersal rules were formulated by considering the abundance of grasshoppers and grasses and their interactions within both potential source and sink cells, habitat conditions of sink cells, and spatial isolation (or connectedness) between source and sink cells. A case study was conducted at a sample landscape in Xianghuangqi County, Inner Mongolia, China. The temporal variations of the modeled grass biomass and grasshopper density were consistent with actual variations. The modeled densities were within the measured ranges for most of the cells. The estimation accuracy was higher for the 4th and 5th instars than for adults, and was higher for cells with higher initial densities (not lower than 3 ind m^{-2}). The modeled results showed that the main factors influencing grasshopper density differed for different instars. During the 2nd and 3rd instar, grasshopper density depended on the number of hatched nymphs and their mortality. During the 4th instar, habitat suitability determined the density threshold that caused grasshoppers to disperse and the potential sink or source cells. This resulted in different density variations between the cells with initial densities >6.0 ind m^{-2} and those with densities <6.0 ind m^{-2}. During and after the 5th instar, grasshopper density was very stable due to the slightly decreasing habitat suitability. The modeled results are expected to provide a scientific basis for predicting grasshopper dynamics and controlling grasshopper plagues in heterogeneous spaces.

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1. Introduction

The Inner Mongolian grasslands are the largest in China and represent a typical Eurasian semiarid ecosystem. Over the past few decades, desertification due to climate change and overgrazing has deteriorated these grasslands, creating favorable habitats for grasshoppers. Since 2000, grasshopper outbreaks have been common across large areas (Liu and Guo, 2004; Zhang et al., 2015). Therefore, it is necessary to precisely predict the location, scope, and degree of grasshopper infestations (Shen et al., 2015; Zhang et al., 2015).

A number of studies have been conducted on grasshopper physiology and ecology in Inner Mongolia (e.g., Chen et al., 2006; Fan et al., 1997; Kang and Chen, 1992; Lu et al., 2005; Ma, 1964). However, most studies have focused on temporal and not on the spatial dynamics. Studies on dynamics have been conducted within individual plots or patches, whereas dynamic models presuppose homogeneity and should be considered point models without any spatial extension. Furthermore, most of these studies did not explicitly link ecological processes to spatial patterns, limiting their ability to provide insights into spatial grasshopper–plant interactions. Nonetheless, such spatial patterns are crucial for understanding and predicting population changes (Chen et al., 2011).

Modeling the spatial dynamics of a population is an ambitious and often a challenging task. Early models introduced the concept of reaction-diffusion systems from physical sciences and used partial differential equations to describe the spatiotemporal dynamics

of state variables (Blackwell, 2007). However, because they assume processes are homogeneous, these early models failed to consider the effects of spatial heterogeneity and local spatial interactions that could be crucial to understanding complex ecosystem dynamics (Chen et al., 2011).

Cellular automata (CA) are a class of complex system models that allow spatially explicit ecological processes to be simulated (Cannas et al., 1999; Hogeweg, 1988; Perry and Enright, 2007; Vinatier et al., 2011; Wang et al., 2003). CA models typically consist of a grid of discrete cells with explicit spatial locations. Each cell is characterized by finite and discrete states describing physical or biological properties. The states of a cell are updated at discrete time steps according to a set of local transition rules that depend on the states of the cell and its neighbors (Balzter et al., 1998). Spatial heterogeneity is exhibited by specifying the related spatial representations of each cell and the spatial relationships between adjacent cells. In addition, a CA model simulates spatiotemporal evolution in a "bottom-up" approach (Grimm et al., 2005; Li et al., 2007). This approach focuses on dynamic processes at a local scale, from which the dispersion pattern at a landscape scale may emerge collectively over time.

Dispersal is important for flying insect populations to survive unsuitable habitat conditions or overcrowding (Ciss et al., 2013) but is often difficult to measure. With simple computational rules and an explicitly spatial approach, CA approaches have been applied to modeling insect populations, with dispersal or the outbreak process as a primary focus. Zhou and Liebhold (1995) developed a series of CA transition probability models to predict the spatial dynamics of gypsy moth (*Lymantria dispar* L.) outbreaks. By incorporating neighboring locations, spatial variation in forest susceptibility or defoliation frequencies, and egg mass counts in their models, they could increase the precision and accuracy of predictions. Pukkala et al. (2014) developed a CA model for the potential spread of the pinewood nematode (*Bursaphelenchus xylophilus*) in Europe by human-mediated transportation, flight direction and distance from its carriers in pine forests, and climate change. Bone et al. (2006) revealed that tree mortality patterns caused by infestations of mountain pine beetle (MPB) could be modeled using a fuzzy-constrained geographical information systems (GIS)-based CA model. Simpson et al. (1999) stated that CA models allow the mechanisms by which vegetation distribution at a local scale affects population dynamics to be explored.

In our study, we constructed a CA model of the single species population dynamics of *Oedaleus decorus asiaticus* Bei-Bienko in a steppe habitat. The main aim was to investigate what in the environment drives the evolution of grasshopper abundance (temporal pattern) and distribution (spatial pattern), and from which the transition rules (especially dispersal rules) were formulated. Although the present study focuses on model design, not model implementation, we used a case study as model validation.

2. Material and methods

2.1. Study area and grasshopper species

The study area was in Xianghuangqi County, Inner Mongolia (41°56′–42°45′ N, 113°32′–114°45′ E). The climate, terrain, vegetation, and soil conditions have been described in Shen et al. (2015) and Zhang et al. (2015).

The area was mostly dominated by the grasshopper species *O. d. asiaticus*, but *Dasyhippus barbipes* Fischer-Waldheim, *Bryodema luctuosum* Stoll, and *Myrmeleotettix palpalis* Zubowsky were also present. The present study considered only *O. d. asiaticus*, a primary pest in the grasslands of the northern China. *O. d. asiaticus* is an oligophagous insect that prefers feeding on grass, including *Stipa*

krylovii Roshev., *S. grandis* P.A. Smirn., *Cleistogenes squarrosa* (Trin.) Keng, and *Leymus chinensis* (Trin.) Tzvelev (Chen, 2007).

O. d. asiaticus is univoltine. Generally, the 4th and 5th instar nymphs and adults occur in early July and the density peaks in mid- to late July. Adults oviposit in the top 5 cm of the soil in late July or early August, dying soon thereafter. Eggs have an obligatory diapause that lasts the entire winter, and nymphs hatch in early to mid-June the following year (Chen, 2007; Zhou et al., 2012).

The morphological characteristics of *O. d. asiaticus* determine its dispersal ability (Yan and Chen, 1998). The 1st, 2nd, and 3rd instar nymphs often move between adjacent land surfaces within a site, whereas the 4th and 5th instar nymphs and adults may fly to other sites and landscapes within a 15-km range (Chen, 2007). Adults seldom migrate beyond 15 km.

2.2. Cellular automaton model description

2.2.1. Cellular space

The cellular space is a relatively closed system, which means that *O. d. asiaticus* individuals move mostly within the space defined and outside individuals rarely enter the space. It is defined as a regular or irregular two-dimensional matrix of identical square cells. A cell is a modeling unit with spatially homogeneous physical and biological conditions in which individuals can mingle. A GIS raster-based environment provides a spatial framework for discrete cells in the CA model.

O. d. asiaticus individuals disperse uniformly randomly within a cell at any time, but form clusters (social groups) over the cellular space, mostly resulting from spatial heterogeneity in environmental characteristics, especially patches where plants are clumped together. Given that our aim is to explore the spatial dynamics of grasshopper populations within the space, the cell (a homogeneous spatial unit) size should be smaller than the smallest scale of relevant environmental heterogeneity (the size of habitat patches) or the range over which local spatial association of individuals occur (the characteristic scale of local dispersal). Meanwhile, the space extent should be larger than this characteristic scale (Berec, 2002; Dungan et al., 2002).

We conducted a field experiment on the spatial aggregation of *O. d. asiaticus* individuals at a typical sample plot in Aobaoyingol village. Moran's *I* correlogram of *O. d. asiaticus* density showed that individuals were strongly clumped within a range of about 180 m × 180 m surrounding a site, which was the characteristic scale of local dispersal (data not shown). When the range changed from 180 to 210 m, the individuals were randomly distributed. When the range reached 210 m, individuals became widely dispersed. Hence, the cell size should not be larger than 180 m × 180 m and the space extent should not be smaller than 180 m × 180 m.

Cells located near the space boundary have incomplete interactions with neighbors than those in the middle of the space. This phenomenon, termed the edge effect, is a common model artifact (Berec, 2002). To reduce the edge effect, the space is artificially expanded to more cells surrounding the actual edge cells. Therefore, the edge cells become the central ones within their discrete neighbors, so that they have complete interaction with neighbors and can be simulated. Given that the expanded cells outside the boundary are not the actual ones, environmental conditions and grasshopper abundance and behaviors within these cells are considered the same as those within the nearest actual edge cells. The population dynamics within these expanded cells are also simulated, but the results are not analyzed and exhibited.

2.2.2. Neighborhood

The neighborhood refers to the cells in a defined area surrounding each cell that may influence the state of that cell during the next time step. The model assumes that the individuals within a