Ecological Modelling 352 (2017) 1–18

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Predicting shifts in large herbivore distributions under climate change and management using a spatially-explicit ecosystem model

Timothy J. Fullman[a,*,1], Erin L. Bunting[a], Gregory A. Kiker[b,c], Jane Southworth[a]

[a] University of Florida, Department of Geography, 3141 Turlington Hall, P.O. Box 117315, Gainesville, FL 32611, USA
[b] University of Florida, Department of Agricultural and Biological Engineering, 1741 Museum Road, Bldg. 474, P.O. Box 110570, Gainesville, FL 32611, USA
[c] University of KwaZulu-Natal, School of Mathematics, Statistics and Computer Science, South Africa

ARTICLE INFO

Article history:
Received 21 October 2016
Received in revised form 27 February 2017
Accepted 28 February 2017
Available online 11 March 2017

Keywords:
SAVANNA
Management
Climate change
Elephant
Artificial water
Kruger National Park

ABSTRACT

Wildlife managers use a variety of interventions to alter species distributions but it is uncertain how effective these techniques will be under shifting climate. There is growing recognition of the importance of including climate change scenarios into management planning and actions, but this is lacking in many systems. The spatially-explicit ecosystem model, SAVANNA, was used to predict shifts in large herbivore distribution from 2020 to 2079 under scenarios of climate change, water management, and elephant population growth in Kruger National Park, South Africa. Directional persistence was used to indicate where five large herbivore species – elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus quagga*) – were predicted to increase or decrease their density relative to historic conditions. The overlap in herbivore distributions both within and between species was measured to indicate which change agents were likely to influence future distributions as well as when those influences are expected to occur. We found that patterns differed across climate scenarios. Altering artificial water availability had a mixed overall effect on the persistence of herbivore densities across the park, but strongly influenced the overlap in both within- and between-species distributions. Elephant numbers generally only had an influence under the most extreme case of population growth. While management actions at the scale of large protected areas or regions may not be able to directly alter climate outcomes, they have the potential to mitigate other stressors, increasing the opportunity for species and ecosystems to adapt to uncertain climate effects. Simulation studies of future conditions under interacting climate and management, such as presented here, have important potential to inform decision making, but do not remove the need for continued monitoring and adaptive management.

1. Introduction

Wildlife managers have long sought to manipulate animal numbers and distributions to meet management objectives. They have employed a variety of techniques to accomplish their goals, including provision or removal of artificial water (Smit et al., 2007a), fencing (Hayward and Kerley, 2009; Somers and Hayward, 2012), culling (Wasserberg et al., 2009), translocation (Griffith et al., 1989; Batson et al., 2015), and contraception (Garrott, 1995; Miller et al., 1998). In many cases, opinions have shifted over time about which strategies are most effective and which are socially acceptable (*e.g.*, Owen-Smith et al., 2006; Smit and Grant, 2009).

As evidence of climate change increases (Alexander et al., 2006; Gallant et al., 2014), it is becoming evident that climate shifts also have the potential to influence population numbers and species distribution patterns (Chen et al., 2011; McCarty, 2001; McLaughlin et al., 2002; Parmesan, 2006). In systems subject to climate shifts, management uncertainty increases as population changes may enhance or counter management efforts. Many past studies of the effects of management interventions on target species have not considered potential impacts of climate change (*e.g.*, Hilbers et al., 2015; Smit and Grant, 2009; Smith et al., 2010). On the other hand, there is increasing recognition of the importance of including climate change scenarios into management planning and actions (Heller and Zavaleta, 2009) and that predictions of climate change

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* Corresponding author.
E-mail addresses: fullman.tim@gmail.com (T.J. Fullman), bunterin@ufl.edu (E.L. Bunting), gkiker@ufl.edu (G.A. Kiker), jsouthwo@ufl.edu (J. Southworth).

[1] Present address: The Wilderness Society, 705 Christensen Drive, Anchorage, AK 99501, USA.

http://dx.doi.org/10.1016/j.ecolmodel.2017.02.030

impacts may provide important benefits to decision making by resource managers (Mawdsley et al., 2009).

Protected areas play an important role in efforts to preserve species in the face of climate change (Hole et al., 2009; Mawdsley et al., 2009), even though they may not remain effective for all species (Hannah et al., 2005). At the same time, protected areas are often subject to wildlife and ecosystem management. This creates a need to simultaneously consider the effects of management efforts and climate change on species of conservation concern. Scenario analyses exploring a range of potential outcomes can be used to reduce management uncertainties due to climate change (Glick et al., 2011; Jones et al., 2016). The complexity of ecosystems and their responses under multiple scenarios makes systems modeling a key tool in such analyses (Walker et al., 2003).

Kruger National Park (KNP) is one of the most highly monitored and managed protected areas in Africa. As such, it presents an excellent opportunity to test the effects of climate change and management on species. KNP protects a wide diversity of plant and animal species, including numerous large herbivores. The African elephant (*Loxodonta africana*) is perhaps the best known KNP herbivore and is highly sought by tourists across South Africa (Kerley et al., 2003; Lindsey et al., 2007). Elephants are ecosystem engineers and influence a wide array of ecological processes (Kerley and Landman, 2006). However, high densities of elephants have been linked to declines in biodiversity of both plants and animals (Cumming et al., 1997; Landman et al., 2008; Penzhorn et al., 1974; Valeix et al., 2007b) and elephants may come into conflict with local people (Metcalfe and Kepe, 2008; Sitati et al., 2003). As a result, elephants are at the center of management debates. One of the major issues regarding elephant management revolves around identifying and maintaining the “ideal” number of elephants within the park that meet tourist expectations and sustain ecosystem function without threatening key species or degrading habitats (Owen-Smith et al., 2006). From 1967 to 1994 elephants were culled in KNP with a goal of maintaining around 7000 individuals (Cumming and Jones, 2005; Owen-Smith et al., 2006). More recently, growing recognition of the importance of heterogeneity in savanna systems, and concerns that maintaining a constant number of elephants may actually reduce diversity and ecosystem resilience (Balfour et al., 2007; Gillson and Lindsay, 2003; Owen-Smith, 2004; Walker et al., 1987) have led to a shift in focus to managing the spatial distribution of elephant impacts rather than absolute numbers (Owen-Smith et al., 2006).

Artificial water provisioning is a major management strategy used to manipulate distributions of elephants and other herbivores in KNP (Shannon et al., 2009; Smit et al., 2007a). Hundreds of artificial water points, fed by boreholes that pump water from the ground (Smit and Grant, 2009), have been constructed in KNP over the last century for a variety of reasons, including enhancing game viewing and protecting rare species from drought (Owen-Smith et al., 2006; Parker and Witkowski, 1999). While initially viewed as providing a variety of important services, artificial water later was blamed for problems such as the decline of rare antelope and local degradation of vegetation (Harrington et al., 1999; Smit and Grant, 2009). As a result, recommendations have been made to close a number of the artificial water points in the park (Smit and Grant, 2009). There is a need to better understand and predict the influences of artificial water manipulation and elephant numbers on large herbivores of KNP, especially in light of climate change.

We employ the spatially-explicit ecosystem model, SAVANNA (Coughenour, 1993), to evaluate predicted shifts in large herbivore distribution under scenarios of climate change and management in KNP. We investigate how densities of five large herbivore species vary over space compared to historic levels to explore how intensity of utilization by each species is affected by three change agents: climate change, water management, and elephants. We then explore how these changes occur temporally across scenarios to indicate both which change agents exert a strong influence on future distributions as well as when those influences are expected to occur.

2. Material and methods

2.1. Study area

Kruger National Park (KNP) lies along the eastern border of South Africa (Fig. 1). The climate of KNP features distinct wet and dry seasons with the dry period occurring from May to September (van Wilgen et al., 2004; Wessels et al., 2006). During this time, seasonal waterholes and rivers dry out, leading to altered distributions of water-dependent species (Thrash, 1998). Geology broadly divides KNP in half with the western portion dominated by relatively nutrient-poor granitic-derived soils and the eastern portion by nutrient-rich basaltic-derived soils (Fig. 1; Redfern et al., 2003; Thrash, 1998; Venter, 1986). Vegetation is wooded savanna dominated by *Colophospermum mopane* in the north and *Acacia* and *Combretum* species in the south (Venter et al., 2003).

2.2. The SAVANNA model

SAVANNA is a spatially-explicit landscape model. Originally developed to model pastoral regions in Kenya (Coughenour, 1992), SAVANNA has since been applied to a variety of sites around the world, including across Africa (Boone et al., 2002; Hilbers et al., 2015; Kiker, 1998), North America (Buckley et al., 1995; Coughenour and Singer, 1996), Australia (Liedloff et al., 2001; Ludwig et al., 2001), and Asia (Christensen et al., 2003; Christensen et al., 2004). SAVANNA is process-driven and deterministic, attempting to represent realistic ecological conditions and changes. Ecological data inputs on both abiotic and biotic factors feed into a series of interacting submodels for system components such as water budgets, net primary production, fire, and herbivory, providing information over space and time about shifts in landscape properties. For additional details see Hilbers et al. (2015) and Bunting et al. (2016).

Herbivore distributions in SAVANNA are determined based on estimates of habitat suitability that take into account ecosystem features such as forage biomass, water availability, slope, and shade (Coughenour, 1993). The population is redistributed at each time step among the grid cells based on their habitat suitability estimates, giving a density per cell. For details of the SAVANNA herbivore distribution submodel and the species-specific parameters used in this study, see Appendix A in the Supplementary material. Five herbivore species were modeled: elephant, buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus quagga*). While Hilbers et al. (2015) included browsers in their SAVANNA models, we constrained our analyses to grazers and mixed feeders as they are more susceptible to natural population die-offs due to extreme climatic events (Ameca y Juárez et al., 2014), making them of prime interest for modeling under climate change. Roan antelope (*Hippotragus equinus*) were also modeled, but were excluded from further analyses because small population size (<30 individuals) for most of the study period prevented reliable comparisons with other species and raised questions about population viability (Harrington et al., 1999).

2.3. Model scenarios

Herbivore distributions were compared under climate change, water management, and elephant management scenarios. A total of 27 scenarios were run using a fully factorial design (Fig. 2). Model runs covered two periods: a historic period (1990–2009) and a