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Agent-based modeling of hunting and subsistence agriculture on indigenous lands: Understanding interactions between social and ecological systems

Takuya Iwamura [a,b,*], Eric F. Lambin [b], Kirsten M. Silvius [c], Jeffrey B. Luzar [d], José M.V. Fragoso [a]

[a] Department of Biology, Stanford University, USA
[b] Woods Institute for the Environment, Department of Environmental Earth System Science, Stanford University, USA
[c] Gordon and Betty Moore Foundation, USA
[d] Department of Anthropology, Stanford University, USA

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ABSTRACT

Indigenous people of the Rupununi region of Amazonian Guyana interact with their natural environment through hunting and subsistence agriculture. To date the sustainability of indigenous livelihoods has been analyzed by modeling either hunting or forest clearing. Here we develop a holistic model framework with agent-based modeling to examine interactions between demographic growth, hunting, subsistence agriculture, land cover change, and animal population in the Rupununi. We use an extensive field dataset from social surveys, animal observation records and hunting kill locations along with satellite images. The model exhibits feedback loops between a growing human population and depletion of local natural resources. Our model can reproduce the population size of two different villages along with landscape patterns without further calibration. Our model can be used for understanding the conditions of sustainability for indigenous communities relying on subsistence agriculture and hunting, and for scenario analyses to examine the implications of external interventions.

1. Introduction

Much of the Amazon Basin's forest cover and biodiversity is found in areas inhabited by indigenous people (Nepstad et al., 2006; Schwartzman et al., 2000). Modeling the resource and land use dynamics of these people will help us understand their contribution to Amazonian ecosystems, and may also assist indigenous peoples in their design of sustainable management and livelihood plans. Previous efforts to model the sustainability of indigenous people's resource use activities have typically focused on a few aspects of their livelihoods, and often represented the scope of a particular discipline. Some have primarily investigated the sustainability of hunting (Bodmer et al., 1997; Fragoso et al., 2000; Hill et al., 2003; Silvius et al., 2004; Sirén et al., 2004; Damania et al., 2005; Levi et al., 2009), while others have been more interested in land use decisions and patterns of land cover change (Wilkie and Finn, 1988; Brondizio et al., 1994; Deadman et al., 2004; Nepstad et al., 2006; Sirén, 2007). Sustainability, however, hinges on the feedbacks and balances between social and ecological systems, and should be investigated with a holistic framework (Ostrom, 2007). For example, habitat fragmentation can cause the sudden decline of animal abundance around villages, and lead to agricultural expansion to compensate for food loss due to unsuccessful hunting (Bennett, 2002; Damania et al., 2005). A few studies focus on clarifying the connection between hunting and deforestation (e.g, Wilkie et al., 1998), but are unable to incorporate feedbacks between these activities and natural resources due to the dearth of detailed datasets needed to develop and calibrate complex models.

This paper describes our modeling effort for the indigenous communities in the Rupununi region of Guyana, in the Guiana Shield region of the Amazon, where we collected an extensive

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[*] Corresponding author. Woods Institute for the Environment, Department of Environmental Earth System Science, Stanford University, USA.
E-mail address: takuya@stanford.edu (T. Iwamura).

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dataset on social and ecological aspects of the lives, land, biodiversity, and environment of the Makushi and Wapishana people (Luzar et al., 2011). We apply a holistic framework to investigate human-environment interactions, which is under the rubric of social-ecological systems (SESs) (Ostrom, 2009) or coupled human-natural systems (Liu et al., 2007). Our objective is to develop a model to investigate the conditions under which indigenous communities relying on hunting and subsistence agriculture alter their impacts on an ecological system through land use change.

The Rupununi region provides a unique setting in which to investigate such research questions. Its ancient geological history (1.7 billion years) and mixed upland and lowland savannas, forests and wetlands have resulted in a highly diverse fauna and flora (Hammond, 2005). The region supports approximately 20,000 predominantly Makushi and Wapishana indigenous people (Hammond, 2005; Luzar et al., 2012). The indigenous communities remain largely isolated due to their remoteness from Guyanese population centers on coastal areas, to which they are poorly connected by an inadequately maintained dirt road and scattered airstrips. As is the case in other parts of Latin America (Geist and Lambin, 2002; Lambin et al., 2003), impact assessments for the region (Conservation International et al., 2009) find that government-led infrastructure establishment is expected to trigger deforestation in the Rupununi. Land outside of demarcated indigenous territory in this region is federal state land subject to long term leasing including by foreign industries, which makes public land use policies very important in driving land use change.

Our spatially-explicit household simulation model is meant to analyze the feedback between human activities and natural resource systems by using agent-based modeling (ABM) (Gilbert and Troitzsch, 2005). ABM is a bottom up approach to model decision making by individual "agents" to explain macro-scale behaviors (Parker et al., 2003; Brown et al., 2005; Filatova et al., 2013). It is widely used to simulate social behavior, including land use change based on household-level data (Deadman and Gimblett, 1994; An et al., 2001; Evans and Kelley, 2004; Schreinemachers and Berger, 2011). It has been applied in sectors for which a large amount of data is available, such as transportation (Bonabeau, 2002), insurance (LeBaron, 2006), mobile telecommunication (Fricke et al., 2001), health (Lambin et al., 2010; Linard et al., 2009) and computational social networks (Bonabeau, 2002).

Our model takes advantage of the accumulation of ABM literature on household decision making for subsistence agriculture. Deadman et al. (2004) describes land use change among colonist farmers in the Brazilian Amazon based on satellite images and interviews with local people using spatially explicit ABM. An et al. (2005) investigates the dynamism of demographic changes and their impacts on deforestation in giant panda habitats in China. Entwisle et al. (2008) applies ABM to study the interactions between demographic and land use changes in Thailand. Evans et al. (2011) investigates the agricultural transition from subsistence agriculture to rubber production in Laos. Walsh et al. (2013) combines an ABM (Entwisle et al., 2007) with ecological modeling to identify suitable areas for future agricultural expansion. ABM has also been applied to represent decision making by indigenous people regarding land use (Lim et al., 2002; Berman et al., 2004; Deadman et al., 2004; Cabrera et al., 2012). To our knowledge, only Berman et al. (2004) has modeled both hunting and other activities in indigenous communities. Their study in arctic Canada uses an extensive empirical social data set; however, it does not address changes in animal abundance, distribution and diversity.

Our simulation model presents a more holistic framework incorporating indigenous hunting and agricultural activities as well as changes in demography, land cover, and animal abundance, distribution and diversity. It thus contributes to the study of sustainability of indigenous communities and their environments by providing a tool to investigate complex interactions and feedbacks between human and natural systems. For example, a greater involvement in agriculture activities is explicitly modeled as the result of the decision making of each household managing their energy budgets. Efficient energy intake can be achieved through a mix of hunting and agricultural activities. Successful energy intake for each household results in a demographic increase in a village, which then affects animal abundance, distribution and diversity through wildlife metapopulation dynamics, and vegetation succession.

The major constraint to the application of ABM to socio-ecological systems has been insufficient empirical information to parameterize real-world complexity (Robinson et al., 2007; Windrum et al., 2007; Filatova et al., 2013). In our study, we use a wide range of data on indigenous peoples and communities of the Rupununi (Luzar et al., 2011) to parameterize our simulation model, including interview-based surveys of demographic and socio-economic characteristics of all households within the study area, along with field data on animal kill locations, and the diversity, distribution and abundance of animal species (Luzar et al., 2011; Read et al., 2010; Luzar and Fragoso, 2013), and a time series of land cover change from satellite images. The limited connectivity to the outside world of villages means that the entire system can be modeled based on local factors. This enables us to circumvent a "boundary problem" commonly found in other studies where the extent of the modeling effort is arbitrarily defined (Meadows, 2008).

This paper describes the model based on a spatially-explicit ABM to understand interactions between indigenous people and their natural environment in Guyana's Amazon. We seek in to simulate the interplay between subsistence agriculture and wildlife hunting and their impacts on animal populations and landscape through a bottom-up modeling framework. While our model is implemented through rich datasets from fieldwork, remote sensing and literature review, extensive sensitivity analysis is also conducted to show how robust simulation results are to a few unknown parameters. We validated the model with the field dataset for two different villages to examine its relevance to the real-world settings.

2. Modeling approach

2.1. Study area

The Rupununi region of Guyana (W58°6′23″, S3°17′58″; W59°37′22″, S2°6′55″) lies within the Guiana Shield of the northern Amazon region (Fig. 1). The area is difficult to access due to a mountainous terrain, un-bridged river network, and dirt roads that provide only seasonal access to most communities. The land is poorly suited for agriculture due to poor soils and a strongly seasonal flood regime (Luzar et al., 2011). To date, the Makushi and Wapishana people in the area maintain much of their traditional lifestyle, based on hunting of wildlife, fishing and subsistence agriculture, even after long contact with European and later national, non-indigenous socioeconomic systems (Luzar et al., 2012; Luzar and Fragoso, 2013; Read et al., 2010). Their only staple crop is cassava, from which they produce cassava flour that can be stored dry, but often suffers from insect infestation and humidity (Hodges et al., 1985). A large extent of the Rupununi savanna is seasonally flooded and not suitable for cultivation. This flood regime and poor soil traditionally may have limited the population level in the Rupununi (Hammond, 2005). For example, a few years before our fieldwork, rainfall was unusually high and destroyed newly planted fields; the stored cassava flour was used up or spoiled and people were forced to abandon their villages and move to Brazil or Guyana's cities (*pers. comm. with villagers*). Hunting is the major

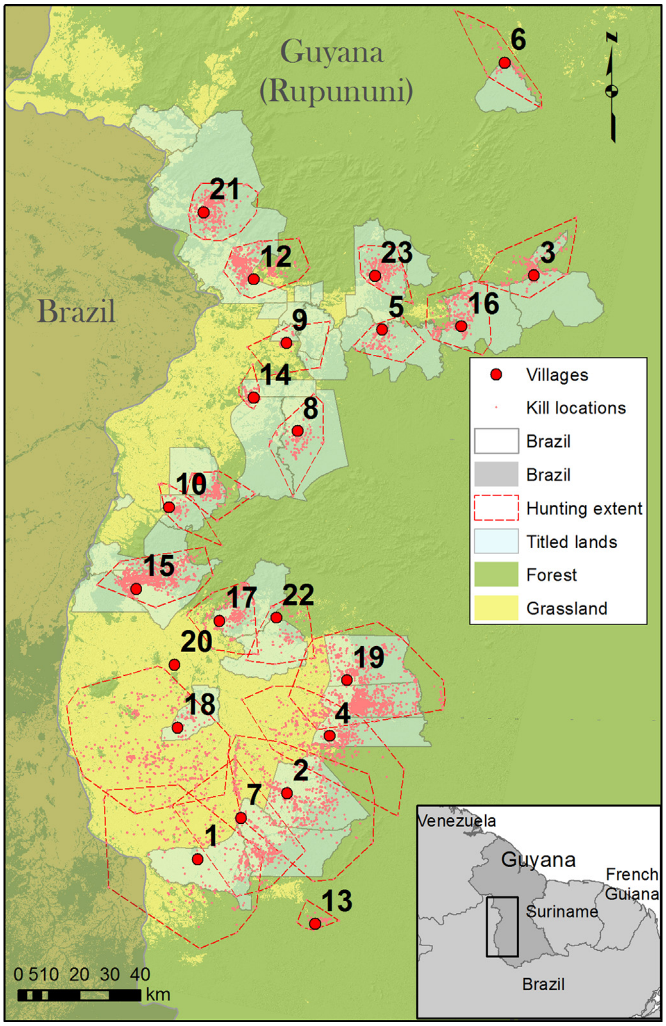

Fig. 1. Map of Rupununi vegetation and villages. Red circles represent the locations of study villages. The numbers represent the village IDs. The pink dots are kill locations. The red broken lines delineate the collective hunting territories of the village hunters based on all kill locations for that village. The blue polygons delineate the boundary titled to the villages by the federal government. Background color indicates the land cover based on Landsat TM images, where the grassland is represented in yellow and the forest in green.

source of protein, and usually is conducted by the male head of the household. Fishing is important for villages near rivers, but it is generally limited to the dry season as catching fish is difficult when the river is flooded. Indigenous cosmology and spiritual practices remain important aspects of Makushi and Wapishana culture, and shamans or healers continue providing guidance on resource use and healing of illness in many communities (Luzar et al., 2012; Luzar and Fragoso, 2013).

The 2006 Amerindian Act sets out indigenous land and other rights for Guyana's indigenous peoples with appointment of an indigenous leader as its governor. Land titled to indigenous people in the Rupununi tends to be focused on single villages (Fig. 1). As these village-titled lands are dispersed among extensions of government-owned public lands, the possibility exists that these areas will become highly fragmented with future developments. These small titled areas are thus vulnerable to external influences. The Rupununi borders large agro-industrial development projects in the neighboring Brazilian state of Roraima and the Guyanese government has endorsed the Initiative for the Integration of Regional Infrastructure in South America (IIRSA) to promote the regional development and integration of rural and urban areas. Under IIRSA, the Guyanese government proposed a project to upgrade (i.e., pave) the major dirt road, which cuts through the Rupununi region to connect the agricultural areas in Brazil with Georgetown, Guyana's capital and a port city. This project is expected to promote deforestation (Conservation International et al., 2009). The government of Guyana also seeks to conclude partnerships with agricultural corporations for large-scale agricultural development in the natural savannas, while protecting forest cover under a national Low Carbon Development Strategy (Ebeling and Yasué, 2008).

2.2. Dataset

2.2.1. Social dataset

Trained indigenous field technicians collected social data over 3 years (Read et al., 2010; Luzar et al., 2011, 2012; Luzar and Fragoso, 2013) under the guidance of senior project staff. A complete survey among all 9900 residents in each of the 23 communities was conducted to describe basic demographic status (Table 1). Highly detailed socio-economic information was collected for the 1307 households of the 23 communities. This study uses a subset of the survey datasets (Table 2) to parameterize the model.

2.2.2. Ecological dataset

Information on animal species, distribution and abundance was collected for 8 transects at each of 23 villages and 4 control sites (Luzar et al., 2011). Transects were equally apportioned among distances near a village (0–6 km) or far from a village (6–12 km), to sample areas with different hunting intensities, mediated by the distance the hunter needs to travel (Luzar et al., 2011). Field technicians collected data twice per month for 3 years. This dataset includes over 47,000 observation records and 85,000 sign records for 275 species in the region. Carbon content of soil and vegetation are also estimated from data collected by indigenous technicians along subsets of these transects (unpublished data). Data from

Table 1
Study villages in the Rupununi.

Village ID	Established Year	The number of households	Bushmeat
1	1930	111	2.00
2	1910	221	2.77
3	1950	49	1.77
4	1940	112	2.60
5	1980	37	2.46
6	1980	33	2.06
7	1920	190	2.48
8	1970	102	2.69
9	1930	22	1.95
10	1930	69	2.79
11	1930	106	2.58
12	1950	85	2.35
13	1985	27	2.00
14	1940	37	2.92
15	1930	21	1.52
16	1950	47	1.07
17	1910	110	2.94
18	1910	82	2.49
19	1920	248	2.47
20	1960	14	2.07
21	1920	33	1.73
22	1960	54	2.13
23	1940	34	2.41

Numerical ID rather than names are used to protect confidentiality of the communities. Rough estimates when villages were established are shown as "Established Year". "The number of households" are based on our field dataset. "Bushmeat importance" is a village-level average of the measurement for how important bushmeat is for each family as opposed to other protein sources (e.g. fish, domesticated animals), where 1 is most important and 3 is least important (derived from our unpublished data).

Table 2
Parameters used in the model.

Model	Parameters	Values	Source
Demography	Longevity of household	42 years	Field data
Demography	Fecundity rate	Age specific	Guyana Census 2002
Demography	Child mortality rate	14%	Guyana Census 2002
Demography	Number of initial colonizers	NA	NA (Used to initialize simulation. Examined by a sensitivity analysis)
Energy	Target energy requirement	1,276,560 kJ/mo	WHO 1991, Cordain et al., 2000
Energy	Minimum energy requirement	1,058,400 kJ/mo	FAO 2008
Energy	Max% of energy intake from protein	35%	Speth, 1987, Cordain et al., 2000
Energy	Unit energy per bushmeat	7240 kJ/kg	Cordain et al., 2000
Energy	Unit energy per crop (cassava flour)	1384 kJ/kg	Grace, 1977 (355 cal/100 g Goplek)
Energy	BMR (Basal Metabolic Rate)	279.6 kJ/h	WHO 1991
Hunting	Walk speed in grassland	4 km/h	Field observation
Hunting	Walk speed in forest	2 km/h	Field observation
Hunting	Maximum hours/day spent hunting	11 h	Field data
Hunting	Maximum number of trips in a month	8–20	Field observation. (Examined by a sensitivity analysis)
Hunting	Maximum animals hunted in one trip	3	Field data
Hunting	Bushmeat ratio per bodymass	85%	Cordain et al., 2000
Hunting	Hunting success rate	10 - 90%	Estimated as 33%: Sensitivity analysis
Hunting	BMR unit for walking in jungle	5.7 BMR	WHO 1991 (Annex 5)
Hunting	BMR unit for walking (with 10 kg load)	3.5 BMR	WHO 1991 (Annex 5)
Hunting	BMR unit for hunting	3.6 BMR	WHO 1991 (Annex 5)
Agriculture	Yield per Ha	6056kg/Ha	Blair, 2010
Agriculture	Conversion rate to farinha manioc	15%	Grace, 1977; Dufour, 1994
Agriculture	Time for clearing forest (Ha)	441	Pascual 2002, Pascual & Barbier, 2001
Agriculture	Time for harvesting crop	20	Total labor time (638) −clearing (441) −weeding (157)*0.5
Agriculture	Time for planting crop	20	Total labor time (638) −clearing (441) −weeding (157)*0.5
Agriculture	Time for weeding	157	Barton et al., 2001
Agriculture	BMR unit for walking with 10 kg load	3.5 BMR	WHO 1991 (Annex 5)
Agriculture	BMR unit for clearing	7.9 BMR	WHO 1991 (Annex 5)
Agriculture	BMR unit for weeding	2.5 BMR	WHO 1991 (Annex 5)
Agriculture	BMR unit for planting root crop	3.9 BMR	WHO 1991 (Annex 5)
Agriculture	BMR unti for harvesting root crop	3.5 BMR	WHO 1991 (Annex 5)
Land cover	Land class (forest, grassland, water)	Spatial	Remote sensing, Landsat TM
Land cover	Cell size	2–10 Ha	Sensitivity analysis
Land cover	The extent of hunting	Spatial	Construct from hunting records
Land cover	Titled land	Spatial	Field data
Land cover	Time to stop harvesting	3 years	Interview
Land cover	Weeding frequency	3 times/year	Interview
Land cover	Fallow period	5–20 years	Interview (Examined by a sensitivity analysis)
Land cover	Carbon in forest	213 tC/ha	Field data
Land cover	Carbon in secondary forest	170 tC/ha	Field data
Land cover	Carbon in grassland	33 tC/ha	Field data
Animal pop.	Dispersal ranges	See Table 3	Schloss et al., 2012
Animal pop.	Intrinsic population growth rate	See Table 3	Robinson and Redford 1986, Hailey, 2000
Animal pop.	Population density	See Table 3	Field data, Silvius and Fragoso 2003, Ojasti 1996
Animal pop.	Body mass	See Table 3	Robinson and Redford 1986, Hailey, 2000
Animal pop.	Probability of non-dispersal	90%	Estimation (Examined by a sensitivity analysis)

transects are used to derive village specific game animal densities and carbon stocks, and these densities are used to estimate game animals abundances over the territory of villages in our model.

2.2.3. *Hunting dataset*

Every successful hunt conducted by inhabitants of the villages is recorded monthly (Fig. 1) (Read et al., 2010; Luzar et al., 2011). Hunting records include the name of the hunter, the location of the kill, species killed, and duration of the hunting trip, for a total of over 8000 kills recorded. Kill locations are used to estimate the extent of the hunting range for each village by calculating a convex hull polygon.

2.2.4. *Remote sensing*

We use Landsat TM Images for September 1998, October 2005, and August 2011 (Path 231, Row 57 and 58). After removal of cloud cover, we classify these images into four classes – forest, bush, grassland and water body. Our interest focuses on forest and grassland categories, where we measure change in forest cover and the expansion of grasslands as a result of vegetation clearing. Indigenous communities in the Rupununi prefer forests that are mature enough for soil fertility to be established for farming (*pers. comm. with villagers*). Accuracy assessment indicates that our classification is accurate except for the bush class (Table S1). This class is intermediate between the forest and grassland in terms of photosynthetic activity, and is sometimes misclassified as either grassland or forest. We have conducted change detection only with the forest class to determine the amount of deforestation and forest regeneration during the period covered by the image time series. Change detection is processed by change magnitude (CM) analysis after tasseled cap conversion (brightness, greenness and wetness) (Coppin et al., 2004). The threshold of the CM is determined by comparison between the statistical distributions of the CM and the areas of apparent change that are detected. Vegetation classification is used to set the land cover parameters for the simulation villages, as well as to determine realistic rates of forest conversion over long time periods.

2.3. *Model description*

ABM is a bottom-up modeling technique, where each autonomous entity, such as an individual person or animal, is expressed as a set of parameters and behavior rules (Railsback et al., 2006). In our spatially-explicit model, a simulation is carried out in two dimensional gridded cells, with a value to represent the condition of the land (e.g., land cover, biomass, etc.) (Castle and Crooks, 2006; Crooks and Castle, 2012). These values can be modified based on a certain rule (e.g., forest transition), often referred to as cellular automata (CA). We develop our model (Fig. 2ab) by using Netlogo, the programming environment specialized for spatially explicit ABM (Wilensky, 1999). The simulation model is described below following the ODD (Object Design and Details) protocol (Grimm et al., 2010).

2.3.1. *Purpose*

The overarching purpose of the model is to understand the mechanism of social and ecological interactions and feedbacks on lands held by indigenous people. Our household-level simulation explores feedbacks between land use by indigenous people and ecological systems (wildlife species diversity, abundance and distribution, and carbon stocks) (Fig. 2a). It is conducted to understand how an initially small population of humans dependent on local natural resources through hunting and subsistence agriculture develops into a larger village with more extensive agricultural areas. We analyze the feedbacks between human demographic change and the changes in land cover and animal abundance, distribution and biodiversity as mediated by hunting and agricultural processes.

2.3.2. *State variables and scales*

There are four types of agents in this simulation: landscapes ("patches"), villages, households, and animal species. The household agent provides fundamental ("low-level" as ODD defines) mechanisms. The behavior of individual households is modeled and the consequences of their decisions are analyzed at the village level. The mechanism at the core of the household agent is energy budget accounting, where each household tries to satisfy its members' energy requirements by a mix of hunting and cultivation (Bailey et al., 1989; Cordain et al., 2000; Sirén, 2006). There are two levels of energy requirements: (1) the target energy requirement, which corresponds to the recommended energy intake (WHO, 1991), and (2) the minimum energy requirement, which defines a state of malnutrition (FAO, 2008). In our model, each household agent tries to achieve the target energy requirement every month. If they cannot achieve the minimum energy requirement, the household is considered to be undernourished and leaves the study area. Hunting and subsistence agriculture complement each other to achieve the required energy intake (Cordain et al., 2000; Fischer-Kowalski et al., 2011). When hunting alone cannot meet the target energy requirement intake, the household can compensate for the shortage from the surplus of a staple crop (stored cassava flour) and expand their cultivated area to increase production for the following year. A simplified model structure is presented in Unified Modeling Language (UML) (Fig. 2b).

We assume that a household consists of five family members (1 adult male, 1 adult female, 1 boy, 1 girl, and 1 elder) based on the mean family size (5.03) and number of children (2) from field observations. The total energy requirement of such a household is 1,276,560 kJ (304,901 kcal) per month (WHO, 1991). Cordain et al. (2000) analyzed energy intake for 64 indigenous societies relying on wild meat and concluded that a maximum of 35% of their energy intake comes from meat. In our simulation, each household tries to satisfy up to 35% of their total energy intake (446,796 kJ/month) through hunting. A household cultivates lands to produce enough cassava flour to cover the base non-meat energy intake, or 65% of their total target energy requirement (829,764 kJ/month). The minimum energy requirement (the malnutrition limit) of a family with five members is 1,058,400 kJ/month. If they cannot achieve this amount from both wildlife hunting and consuming stored cassava flour, they are considered undernourished.

Each patch agent represents a unit (cell) of the landscape. Collectively, they define the geographic boundary of the model. The most important attribute of patch agents is their land cover type: forest, grassland, water body, or cultivated area. Patch agents can transition from one cover type to another, following ecological succession. Patch agents also represent other important attributes such as the extent of hunting for each village, and the political border between Guyana and Brazil. The boundary of the simulation area is defined by a 10 km buffer beyond the extent of hunting of each village.

Village agents represent the location of communities and have a human population with cultural and socio-economic attributes. Village agents contain household agents as their members, and thus aggregate the low level variables of household agents such as number of members, energy intake from bushmeat and cassava flour, cultivated area, and walking distance for hunting of each household. A village agent also contains a set of patch agents that define its hunting territory and titled land.

Animal agents are responsible for the population increase and dispersal of the 10 most hunted animal species by indigenous people in the Rupununi (Table 3). Each animal agent is characterized by biological traits such as species, body mass, intrinsic rate of population increase, population density, home range size, and dispersal range. Animal agents represent either individuals or groups of animals depending on the species. When the species' average home range is larger than the size of a patch, then an agent represents an individual. Otherwise a patch can contain several animals, the exact number depending on the species' population density. Herding animal species (e.g., white-lipped peccary, *Tayassu pecari*) are represented by a single agent that represents multiple individual animals.

2.3.3. *Process overview and scheduling*

The model represents five important processes related to land use: hunting, changes in cultivated area, demographic changes, animal species meta-population dynamics, and vegetation succession (Fig. 2). Interactions between social and ecological systems emerge from changes in human and animal species populations, and in land cover. Shifts in the relative importance of bushmeat and staple crops (stored cassava flour) also emerge from macro scale patterns such as animal diversity and distribution, and land cover conversion. Animal abundance and distribution is mainly influenced by land cover change, which is determined by the size of the human population and the extent of land cover change.

Simulations are performed along discrete time steps, following a yearly and monthly cycle. Human and animal species populations change at the end of a year according to the population increase rules. A household may leave the village each month if they don't meet the minimum energy requirement. Animal population may also decrease each month due to the elimination of individuals caused by hunting (see the "sub-models" sections for the details.) The importance of hunting and the amount of crop consumption may change every month. A simulation ends after 100 years or when no household remains in the landscape. The oldest village in our study region is 95 years old.

Interactions between the sub processes (sub-models) are important to better understand the feedbacks between them. In our model, these processes interact through two channels: population change and land cover change. For example, when indigenous communities increase their population, they hunt more animals and convert more forest to cropland. Thus human population change can directly decrease animal populations. Also, when a forested region is deforested and fragmented, the carrying

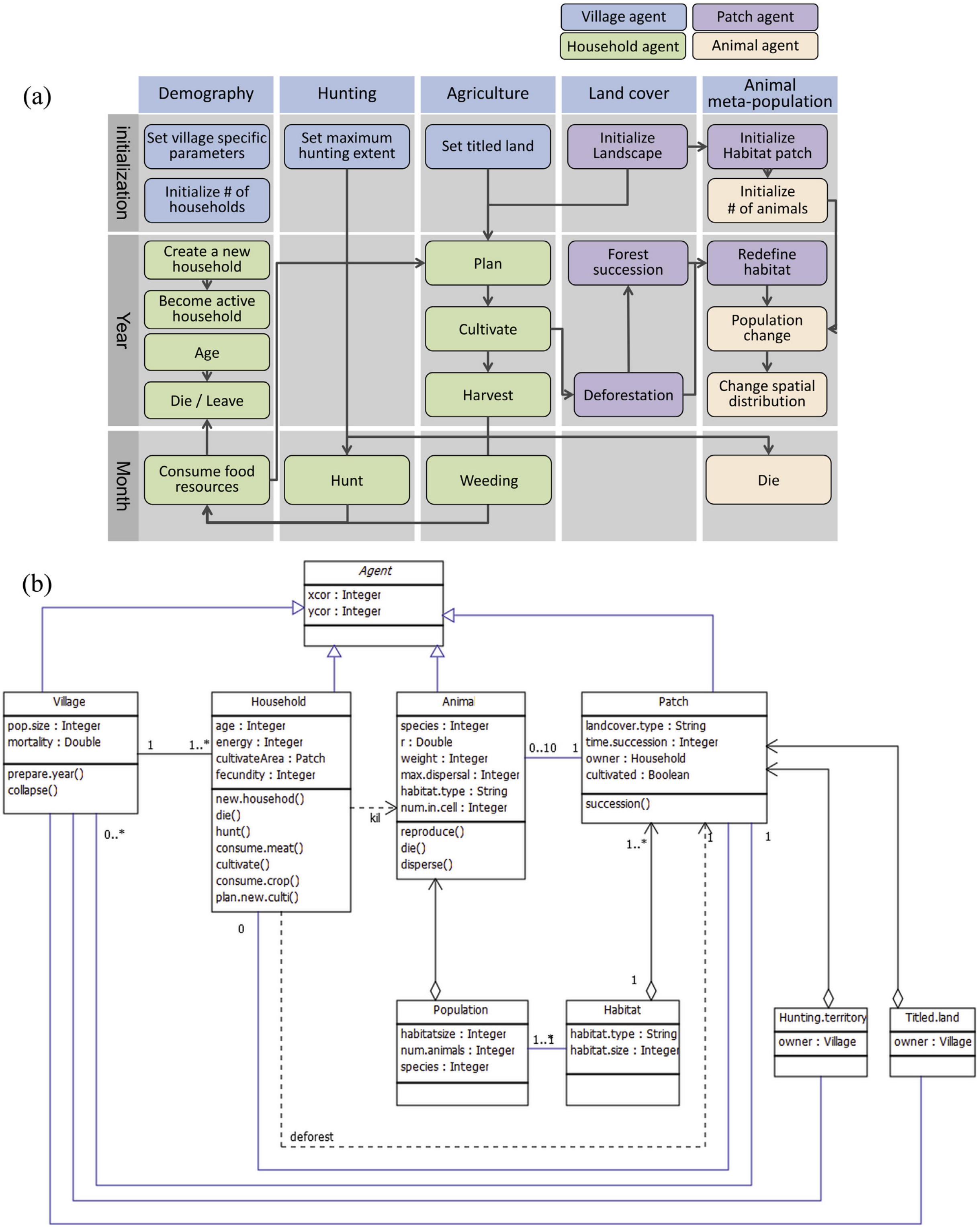

Fig. 2. Process overview and model structure. a) Process overview: The rectangles with round corners represent the activities of different agents in our model. The types of agents are shown in different colors (blue = Village agent, green = Household agent, purple = Patch (cell) agent, pink = Animal agent). The five columns represent the five sub-models (Demography, Hunting, Agriculture, Land cover change and Animal meta-population). Three rows indicate the unit of scheduling (initialization, year and month). The arrows between the rectangles with round corners indicate the sequences of activities. b) Model structure: The model structure is represented according to UML. The attributes and operations of each class (agents) are simplified for display purpose. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Animal species used in the model.

Species name	Body mass	Pop. Increase rate	Home range (Ha)	Density (/km^2)	Hunted ratio	Dispersal velocity (km/year)	References
agouti (*Dasyprocta leporine*)	2.86	0.67	1.7	58.82	0.135	2.33	a (average of 6 spp; body mass, dispersal), b (intrinsic rate), c (homerange, density)
paca (*Cuniculus paca*)	8.2	0.67	2.5	40.00	0.134	4.88	a (dispersal), b (body mass, *r*), c (homerange, density)
White-lipped peccary (*Tayassu pecari*)	29	0.84	6600	7.58	0.104	7.36	a (dispersal), b, g (density)
armadillo sp. (Dasypodidae)	4.99	0.39			0.094	5.4	a (dispersal; nine-banded armadillo), b, g (density)
collared peccary (*Pecari tajacu*)	18	1.25	1090	0.92	0.090	8.42	a (dispersal), b, g (density)
Tortoise sp. (*Chelonoidis* sp.)	4	0.14	17.1	5.86	0.084	5.4	a (dispersal, armadillo as surrogate), d, e (*r*: Spur-thighed tortoise), g (density)
White-tailed deer (*Odocoileus virginianus*)	40	0.73	153.7	0.65	0.053	8.87	a (dispersal), b, g (density)
Red brocket deer (*Mazama americana*)	26	0.4	52.2	1.92	0.049	6.92	a (dispersal), b, g (density)
capybara (*Hydrochoerus hydrochaeris*)	31	0.69	105	0.95	0.021	8.42	a (disperse, collared peccary as surrogate), b
Lowland tapir (*Tapirus terrestris*)	149	0.2	330	0.30	0.020	8.87	a (dispersal, white-tailed deer as surrogate) b (body mass, intrinsic rate), f (carrying capacity), g (density)

The animal species used in our simulations and their ecological characteristics. References are as follows: a. Schloss et al., 2012; b. Robinson and Redford, 1986; c. Beck-King et al., 1999; d. Souza-Mazrek et al., 2000; e. Hailey, 2000; f. Brooks et al., 1997; g. Field data.

capacity for animals is lowered, causing population decline. A household may increase its cropland, when animal populations decline and hunting is increasingly difficult. This, combined with a larger number of households in a village, further promotes deforestation and landscape fragmentation.

2.3.4. Design concepts

Emergence/Adaptation: The feedbacks between the social and ecological system emerge as a result of spatial interactions between indigenous people, hunted animals, and land cover. Household agents can switch between hunting and cultivation based on their energy budget.

Objective/Fitness: The household agent's objective is to satisfy the target energy intake (upper threshold). They also avoid energy levels below the malnutrition level (lower threshold), defined by the WHO/FAO (see *State variables and scales*). They "leave" the village and disappear from the simulation once their energy is below the malnutrition threshold after they consume the stored cassava flour.

Prediction/Sensing: Each household decides how much land they cultivate the following year to satisfy the target energy intake (upper threshold) based on the previous two years' bushmeat consumption. They are also aware of their current energy level and how much they obtain from hunting. Household agents can sense if the landscape cells around their own location are within their hunting territory or not. They can also sense which species of animals are in the cell that they move into.

Interaction: Household agents directly interact with animal agents through hunting. They also indirectly interact with animals through the fragmentation of habitats caused by agricultural activities. Household agents can communicate with each other by noticing other agents' hunting success rate (e.g., they stop hunting when no animals are being killed by anyone.)

Stochasticity: The initial distributions of animal species are stochastically determined. Animals randomly disperse to a certain cell within each species' maximum dispersal range. Household agents randomly decide which of the cells in their hunting territory to move to when hunting. Hunting success is stochastically determined based on the threshold given by the hunting success rate. If there are several animal species larger than 10 kg in a cell, hunters select which animal to kill in a random fashion. Household agents randomly choose a new parcel of land for cultivation if there are multiple available cells at the same distance from the village.

Collectives: Household agents belong to a village. Cultivated cells belong to the household that cultivates those cells. Contiguous cells of the same land cover type are aggregated into a habitat patch. Animal agents of the same species in the same habitat are aggregated into a "population" in the context of meta-population dynamics. Cells under the titled land of a village belong to that village.

Observation: Demographic trends in the household agents are observed and compared to the real village population. Species composition of animals in the vicinity of a village is tracked in the model to compare with field data. The amount of deforestation in a simulation is also monitored to compare with data derived from satellite images. Changes in the fraction of energy intake by household agents that comes from bushmeat are tracked to observe micro level phenomena. The average size of cultivated area per household is also monitored to compare with field data.

2.3.5. Initialization

We run our model for one village at a time due to computational limits. Animal abundance is set to the maximum density per species found in the field data (Fragoso et al., 2010; Luzar et al., 2011). The number of households in a village is set to five initial colonizing families. In order to represent the landscape before the establishment of a village, we assume that areas that are classified as grasslands in the satellite images were originally forested if they are in non-flooding areas with a slope less than 20% (see Submodels: Agriculture). This allows us to run the model with initial landscape conditions rather than conditions already altered by agriculture. Table 2 presents all the input parameters of the model.

2.3.6. Submodels

2.3.6.1. Land cover change. Land cover change is modeled as a transition between different land cover types in 2-dimensional raster cells. Each cell is assigned to one of the four land cover types: forest, grassland, water, or cultivated area. We examine different cell sizes (3–10 ha) to examine how sensitive our model is to the spatial resolution. The topography layer is used to assign areas suitable for cultivation by calculating slope of the area. A household may convert forest to cropland through cultivation (see agriculture section) within the titled land of their village (Fig. 1). We simulate the colonization process of each village with five initial households (see Initialize section). Cultivated areas become fallow after three years of cultivation. After a pre-determined period (see Sensitivity Analysis), a grassland patch transitions to a forest patch, and becomes a secondary forest with a lower carbon value than a mature forest (Nelson et al., 2000). The carbon storage values assigned to different land cover types are based on field data: old-growth forest (230 tC/Ha), secondary forest (170 tC/Ha) and grassland (33 tC/Ha). It is assumed that cells of the same land cover contain the same carbon content.

2.3.6.2. Demographic changes. Demographic changes are simulated as an increase or decrease in the number of households. A household may produce a new household based on the age specific mother-daughter fecundity rate, derived from census data for the Rupununi region (http://www.statisticsguyana.gov.gy/census.html), which provide fecundity rates based on the age of mothers. Our data show that 99.5% of the age distribution of heads of households (typically a male) is within the 21–65 years old range. Typically, spouses are very near in age. In our simulation, daughters create a new household at 19 years of age and, together with their husbands, clear forest patches for their cultivated area. This area is of the same size as that of the mother's household. A household "dies" at the age of 65 years and disappears from the simulation. A household also leaves the landscape when a mix of hunting and agricultural activities does not fulfill its minimum energy requirement.

2.3.6.3. Hunting. Each household in a village hunts within the village hunting territory, which is derived from field-based animal kill locations (Fig. 1). Energy intakes from hunting and subsistence agriculture compensate each other (Fischer-Kowalski et al., 2011). In this study, a household is assumed to prefer hunting animals because it is more energy efficient than crops and because meat is an important source of proteins and iron (Cordain et al., 2000). Energy gain from an animal is calculated based on species weight, the ratio of meat to weight, and energy from a unit of meat. Average weights of animals are defined for each species based on the literature (Robinson and Redford, 1986; Hailey, 2000). We use the estimates of Cordain et al. (2000) for the ratio of energy extraction from animal carcass – i.e., 80% for non-ungulates and 65% for ungulates (Cordain et al., 2000). A household is assumed to consume its hunted animals immediately. Energy gained through this consumption is 7.14 kJ/g (Cordain et al., 2000). Thus we assume that each household has to consume 61.7 kg of meat each month to satisfy 446,796 kJ per month; this is in addition to their non-protein energy requirement described below.

In the model, hunting consists of three stages: searching, killing and consumption. During the searching stage, a household agent moves within the territory randomly, changing its direction stochastically up to 180° at every step. A step is a movement from one cell to another, which consumes energy from the household energy budget. Energy consumption is calculated based on basal metabolic rate (BMR) – i.e., energy consumption during 1 h of sleep. According to WHO, walking requires 3.2 BMR, which means walking consumes 3.2 times more energy than sleeping (WHO, 1991). For each movement from one cell to another, a household agent loses energy, c_{walk}:

$$c_{\text{walk}} = 3.2\beta h_{\text{walk}} \tag{1}$$

β represents the energy consumption of 1 BMR in Joules, h_{walk} is the number of hours required to walk through a cell. h_{walk} depends on the size of cells and the walking speed, assumed to be 3 km per hour. In reality, β changes according to physical characteristics of a person. Here we apply the value of 279.6 kJ/h, which is computed for an average 30-year old male of 170 cm height and 65 kg weight.

If a household agent enters the cell where an animal agent is located, the household agent selectively kills an animal with more than 10 kg in weight at a given hunting success rate (see Verification). If no animal weighing more than 10 kg is located within a cell, a household agent selects the next largest available animal to kill. Larger animals are preferred as they contain a larger amount of meat and have a higher fat-protein ratio, thus higher energy (Speth, 1989; Cordain et al., 2000). Each animal species contains a certain amount of meat (Table 3). A household agent continues hunting if their current energy intake is below the energy requirement threshold, or until the total number of hunting trips reaches the predetermined maximum hunting trips (see Sensitivity Analysis). During each hunting trip, a household can kill up to three animals, up to a total weight of 55 kg.

For each kill, a household loses some energy, c_{kill};

$$c_{\text{kill}} = 3.6\beta h_{\text{kill}} \tag{2}$$

The time required for hunting, h_{kill}, is assumed to be 1 h per animal.

2.3.6.4. Agriculture. In the Rupununi, most of the cultivated land is used to produce coarse flour of cassava, the staple food in the region as well as a cash crop in some villages (Blair, 2010). Swidden agriculture (the clearing and burning of vegetation) is widely practiced, with typically a 10-year fallow period. Each household agent is assumed to cultivate enough land to satisfy their non-protein based energy requirements (65% of their total energy requirement, or 829,764 kJ/month) and to compensate for failed hunting to satisfy protein based energy requirements. The average yield of cassava in the Rupununi region is 6056 kg/Ha, an amount much lower than the national average (Blair, 2010). We apply a conversion factor from raw cassava to cassava flour of 15% to account for energy loss during the process of making cassava flour without modern equipment (Grace, 1977; Dufour, 1994). Each household therefore cultivates 0.74 Ha to satisfy their non-protein based energy requirement, or more when a household cannot fulfill its energy requirement through hunting.

Agriculture is carried out in three steps: planning, clearing/planting, and harvest (Schreinemachers and Berger, 2006). During the planning phase, a household agent calculates how many land cells should be deforested based on the unsatisfied energy intake from hunting in the previous year. Households choose relatively flat non-flooded areas to cultivate. We calculate the maximum slope to be deforested at 20% based on the ASTER Global DEM (Hirano et al., 2003) and the area converted from forest to grassland (see Remote sensing). We also use the land cover data from our previous study in the region (Cummings, 2013; Levi et al., 2013) to delineate flooded areas, which are not appropriate for agriculture. A household agent chooses land patches for farming that are either adjacent to the village or adjacent to their existing cultivated area (Wilkie and Finn, 1988; Deadman et al., 2004). As long as a cell remains cultivated, it continues to produce crops. Interviews revealed that a household can harvest crops for up to 3 years after cultivation begins. The cultivated area is then abandoned and eventually it transitions to secondary vegetation. The ownership right of the land is lost when it is left fallow. In a second step, the household clears the land in the chosen cell. We assume that all households in a village perform long fallow agriculture with a 10-year fallow period (see Sensitivity Analysis). After land clearing, the household plants cassava.

For simplification, a household is assumed only to harvest at the end of the year instead of year round. After the harvest, a household is assumed to consume cassava flour for the next 12 months. Stored dried cassava suffers a 50–70% loss rate after 4 months through infestation by insect pests (Hodges et al., 1985) as well as by decomposition due to high humidity in rainy seasons. Therefore, a household loses the energy for each cultivated plot as follows:

$$c_{\text{clear}} = 5.4\beta \frac{h_{\text{clear}}}{s} \tag{3}$$

$$c_{\text{weed}} = 3.75\beta \frac{h_{\text{weed}}}{s} \tag{4}$$

$$c_{\text{plant}} = 3.9\beta \frac{h_{\text{plant}}}{s} \tag{5}$$

$$c_{\text{harvest}} = 3.5\beta \frac{h_{\text{harvest}}}{s} \tag{6}$$

where s is the size of the cell in hectare. c_{clear} is the energy loss per cell from clearing, c_{weed} is from weeding, c_{plant} is from planting manioc root, and c_{harvest} is from harvesting the crop. h_{clear} is the time required to clear one hectare of forest, which is typically 441 h (Pascual and Barbier, 2001; Pascual, 2002). h_{weed} indicate how long weeding a one hectare plot takes in hours, which is typically 157 h per hectare with hand weeding (Barton et al., 2001). We assume that planting, h_{plant}, and harvesting, h_{harvest}, take 20 h each for one hectare by subtracting the hours for clearing (441 h) and weeding (157 h) from the total amount of hours required for cultivation (638 h, Pascual and Barbier, 2001; Pascual, 2002).

2.3.6.5. Animal meta-population dynamics (population change and dispersal). Change and dispersal in animal populations are modeled in a context of meta-population dynamics (Akcakaya et al., 2004; Polhill et al., 2013). We incorporate ten out of 137 hunted species based on those exhibiting the highest hunting frequencies (Table 3). These ten species represent 86% of the total number of animals killed (8084). Population change is simulated by a logistic function with carrying capacity and intrinsic population growth rate:

$$\frac{dN_{i,j,t}}{dt} = r_i N_{i,j,t-1} \frac{(K_{i,j} - N_{i,j,t-1})}{K_{i,j}} \tag{7}$$

where $N_{i,j,t}$ represents the number of individuals of an animal species i in the habitat j at the time step t, K_{ij} is the carrying capacity of the habitat j for the species i, and r_i is intrinsic population increase rate for the species i. We set the time step as a year and use the rate of annual population increase. A carrying capacity is assigned to each habitat, which is defined as a set of contiguous cells of the same land cover type (forest, grassland or water). Each animal species has its habitat preference (e.g., tapir *Tapirus terrestris* is only found in forests). The carrying capacity of each habitat is calculated based on the maximum population density and the area size of habitat patches:

$$K_{ij} = d_i A_j \tag{8}$$

where A_j is the size of a habitat j and d_i is the population density for species i. Maximum population density is estimated from our database by taking the highest density estimates among 84 transects (Fragoso et al., 2010; Luzar et al., 2011). When the density data are not reliable (e.g., for agouti *Dasprocta leporine*, paca *Cuninculus paca*, armadillo Dasypodidae and capybara *Hydrochoerus hydrochaeris*), they are estimated based on home range records from the literature (Ojasti, 1996; Brooks et al., 1997; Beck–King et al., 1999; Silvius and Fragoso, 2003). The maximum intrinsic rate for population growth and average body weight is taken from the literature for each of the 10 species (Robinson and Redford, 1986; De Souza-Mazurek et al., 2000; Hailey, 2000; Schloss et al., 2012) to represent the background intrinsic rate before hunting further reduces the population. A population is considered extirpated (or no longer available to humans) when the population size reaches 0. A population is also extirpated if habitat area is fragmented to a size smaller than its home range.

Dispersal in this study follows Howard's (1960) and Johnson and Gaines' (1990) definition as "the permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced had it survived and found a mate" (Howard, 1960; Johnson and Gaines, 1990). We assumed that the population that disperses is correlated with the population that would be locally extinct. The potential rate of dispersal for species i in the habitat j is thus calculated as:

$$n_{ij} = \left(r_i N_{i,j,t-1} - \frac{dN_{i,j,t}}{dt} \right) \tag{9}$$

where n_{ij} is the change in the number of individuals of animal species i for the habitat patch j. For each of these potential agents to disperse outside of their habitats, we calculate the distance to disperse d. If there is a cell within the radius of d that is a suitable habitat type and the population of the same species within the habitat is not saturated, the agent can disperse to the cell. We used the modified geometric dispersal model of Miller and Carroll (1989) to calculate dispersal probability based on distance. The distance of dispersal for an animal agent k of species i is calculated as:

$$d_{ik} = D_i \frac{X_k - p_0}{1 - p_0} \tag{10}$$

where D_i is the maximum dispersal distance for species i (Schloss et al., 2012), p_0 is the probability of not dispersing (Miller and Carroll, 1989), and X_k is a random number between 0 and 1. Given the lack of good empirical estimates for p_0, we conducted sensitivity analyses on this parameter.

3. Model evaluation

We evaluate our simulation model in two ways: verification (internal consistency) and validation (external consistency). With verification, we confirm that the system logics, as described above, are correctly represented in the program. This includes a sensitivity analysis on the eight parameters for which we do not have data. We followed the protocol of Pattern Oriented Modeling (POM) (Grimm et al., 2005). POM provides a rigorous framework for model verification and validation for social-ecological systems, where multivariable and complex interactions between variables are the norm (Ostrom, 2009). POM strongly recommends using multiple "patterns" at both macro- and micro-levels of systems (Jeltsch et al., 1997) to examine whether the model represents the real-world dataset to avoid overfitting and artificial reproduction of a macro-level target variable (e.g., population size of a specific village). This ensures that a model represents the micro-level mechanisms as well, rather than just mimicking the macro-level patterns superficially.

3.1. *Verification (Internal model consistency)*

Internal model consistency is examined by sensitivity analysis after removing misrepresentations of the model logic and minor programming errors. We conduct an extensive sensitivity analysis to examine which parameters most influence simulation outputs and evaluate the model's internal consistency. Unexpected changes in system behavior could result either from a surprise relating to the system dynamics, or from a logical or programming error. Sensitivity analysis is especially insightful for this study because we do not calibrate unknown parameters to fit the model output to known values. The sensitivity of our model is analyzed against seven parameters whose exact values are difficult to obtain empirically (Table 2). We are, however, able to approximate fallow period and maximum travel distance based on interviews with villagers conducted by T. Iwamura. Thus, for these parameters, we set a range for sensitivity analyses around these rough estimates. The probability of hunting success can be estimated based on the frequency of usage of guns *versus* bows and arrows from the dataset (Read et al., 2010; Luzar et al., 2011, 2012).

The seven parameters used in the sensitivity analyses are:

1. Cell size, which is expected to affect the level of landscape fragmentation. We conducted the sensitivity analysis for cell sizes of 3, 4, 6, 8, and 10 ha.
2. Hunting success rate: previous studies in Amazonian indigenous communities report hunting success rates of 10% for bows and arrows and 90% for guns (Levi et al., 2009; Shepard Jr. et al., 2012). We estimated the average hunting success per animal pursued in the Rupununi at 33% based on the proportion of guns used in successful hunting trips (Read et al., 2010). We conducted the sensitivity analysis by varying this parameter from 10 to 90%, by 10% increments.
3. Fallow periods: According to our interviews, most villages in remote areas transition to secondary forests after 10 years. We conducted the sensitivity analysis for values of 5, 10, 15, and 20 years.
4. Probability of animals not migrating to other habitat patches: We assume that dispersal to other habitat patches follows the adapted geometric dispersal of Miller and Carroll (1989). We tested the following probabilities for animals not to disperse: 70, 80, 90 and 100%. 100% means all the potential animal agents that exceed carrying capacity of their habitat die instead of dispersing.
5. Maximum number of hunting trips per month: We conducted the sensitivity analysis for 8, 16, and 20 hunting trips per month.
6. Maximum distance between villages and their cultivated areas. In our interviews, this maximum distance is within 2 h commuting time. While villagers often travel by foot, in more developed areas, they may use a bicycle. We conducted the sensitivity analysis for 10, 15, and 20 km.
7. Number of colonizers: We tested 3 different values for the number of households required for successful colonization of a new village: 5, 10, and 15 families.

The simulation results are observed through eight variables that are recorded on an annual basis to evaluate the sensitivity of the model at the individual- (micro) and system- (macro) levels, following POM (Grimm et al., 2005). The system-level behavior is captured by household number and animal abundance (total number of individuals) in the village hunting territory, animal species diversity measured by the Shannon index (Magurran, 2004), and the loss of carbon in the village titled land. The individual-level behavior is captured by the ratio of energy from bushmeat, mean kill weights (the body mass of animal hunted), the average hunting distance between kill locations and the village, and the average area cultivated per household.

3.2. *Validation (External consistency)*

We validate our model by comparing the results of colonization simulations for different villages with the information for these villages derived from fieldwork. Since our model assumes minimum external influences on the system (no markets for goods and labor, no interaction with other villages, no impacts from developments outside of their titled land), validation should be carried out by comparing villages that most represent this closed environment. In the field, we observed that the degree of "development" of a village (e.g., water facility, size of communal buildings) is related to its population size. Villages also tend to be larger when they are older, but with a large variance in village size for similar establishment date (Fig. 3). Long-established villages with small populations are the best candidates for validation, as they are often less open to the outside world. Among these smaller and older villages, we selected those where bushmeat is considered an important component of people's diet. Two villages, Villages 21 and 16 (Fig. 1), are thus chosen to validate our model because they were established more than 60 years before the time of the study and yet contained a small number of households. These two villages have experienced a significant emigration, especially during periods of food scarcity in the village (pers. comm. former village leader, unpublished records). Although these two villages are similar in size and isolation, they are situated in different natural environments.

We validate our model using the same parameter settings for the two villages, and do not perform any artificial calibration of parameters to "mimic" reality. Our model results only derive from the processes represented in the model and parameter values collected in the field. The simulation model is validated with four variables: human population size, average cultivated area, the difference in total number of animals in the near and far areas (0–6 km radius and 6–12 km radius) from a village (see Luzar et al., 2011), and the average distance to kill locations from a village. The number of households and the change in animal diversity, distribution and abundances are macro-scale variables that reflect overall model behavior. The average extent of cultivated areas and the mean distance to kill locations are micro-level variables that verify that the model behaves appropriately. Since the total number of animals is sensitive to the cell size, we validate the relative difference in the number of animals between near and far areas with the relative difference in animal sign data (e.g., tracks and feces) collected in the field (Fragoso et al., 2010; Luzar et al., 2011) in corresponding ranges in our dataset. These values are not used to calibrate the model.

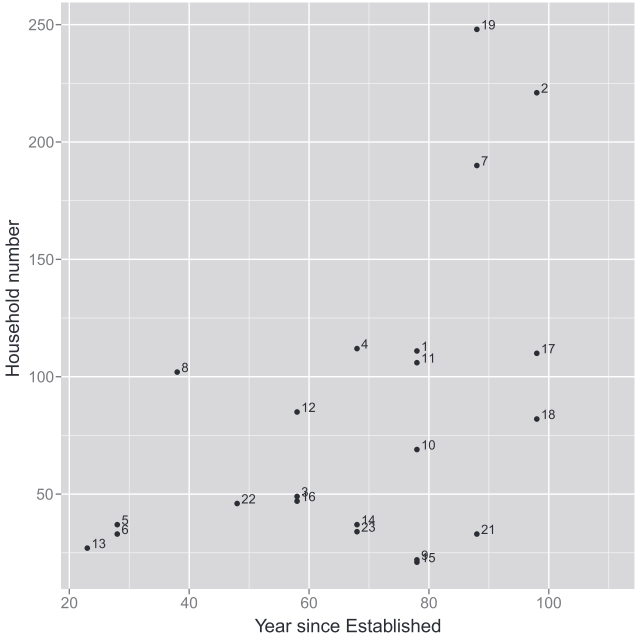

Fig. 3. Established age and the household numbers of villages. The *X*-axis represents the year since establishment of the villages. The *Y*-axis represents the number of households in each village. The numbers are village IDs.

4. Results

Our simulation results show some clear patterns in terms of human–nature interactions for the study region of the Amazon. With the establishment of a human community, animal abundance and biodiversity as well as carbon stocks decrease gradually but slowly. Initially, land conversion is limited to areas near the village (Fig. 4A). Over time, the distance between animal-kill locations increases and the average body mass of killed animals decreases. To compensate for the increasing difficulty of hunting, each household agent increases the amount of area cultivated and consumes more cassava flour. The number of households begins increasing after 20 years as newly established households reach the age of independence. After this point animal abundance and species diversity declines quickly in the hunting territory of a village. Concurrently, households begin to cultivate areas further from their village (Fig. 4B). The species composition of animals in the village's hunted area becomes dominated by smaller bodied species that attain high maximum population densities (e.g., agouti *Dasyprocta leporine*).

When we parameterize the model with the field data, both macro variables (e.g., the number of households, the total number of animals in the hunting extent) and micro variables (e.g., the area cultivated, hunting distances) attain a stable plateau, indicating that the whole system is stabilized at the equilibrium (Fig. 3). This reflects the realistic patterns we observed in the field for smaller villages, where village size have remained stable for 50–60 years. By contrast, with unrealistic values for the parameters, the simulation results do not reach equilibrium (e.g., the number of households increases too rapidly, and the animal populations collapse). At the same time the locations of land conversion show a concentric pattern around the village (Fig. 4C), which was also observed in the field (Fragoso pers. obs.).

4.1. Sensitivity analysis

Similar system responses are observed with all the parameter settings of the sensitivity analysis (Figs. 5–8, S1–3). The values at equilibrium for some of the variables, however, are sensitive to certain parameters of the sensitivity analyses (Table 4). For example, the total number of animals (abundance) and the amount of carbon loss are sensitive to cell size (Table 4), with higher animal abundance and less carbon loss at smaller cell sizes (Fig. 5). In contrast, the number of households and the diversity of species are not particularly sensitive to cell size (Fig. 5, Table 4). Among micro-scale outputs, the average distance between the locations of kills and the village is sensitive to the cell size (Table 4). Average kill distances are smaller at smaller cell sizes (Fig. 5). We have conducted the rest of the sensitivity analysis with an 8 ha cell size to optimize computation resources and simulation outputs.

Model outputs are most sensitive to the hunting success rate (Fig. 6, Table 4). The number of households at the equilibrium increase as the hunting success rate increased from 10% to 40% (Table 4), but those at above 40% hunting success rates converge to the same level with the number of households at the 40% success rate (Fig. 6, Table 4). Animal abundance and diversity were also sensitive to hunting success rate (Table 4). Animal abundance becomes lower at the higher hunting success rate, even though the human population stopped increasing at a 40% success rate (Fig. 6). The species diversity index shows higher values at the highest hunting success rates (80 and 90%) than at medium levels (Fig. 6). All the micro-scale variables are also sensitive to the hunting success rate (Table 4), and they also converge to the same levels at hunting success rates above 40% (Fig. 6).

The length of the fallow period influences the amount of carbon lost (Fig. 7 and Table 4), with carbon loss increasing as the fallow period becomes longer (Fig. 7). The number of households is slightly higher at shorter fallow periods (Fig. 7, Table 4). Animal abundance is also higher with shorter fallow periods (Fig. 7). Among the micro-scale variables, only the average distance between the location of animal kills and the village is sensitive to the length of fallow periods (Table 4).

Model outputs are not sensitive to the maximum commuting distance to cultivated areas, except for very short distances. At the commuting range of 5 km, the number of households remains smaller and bushmeat consumption per family is notably higher than at longer distances (Fig. 8). Animal abundance is higher when people commuted 5 km to their farms (Fig. 8).

Three other parameters – the initial number of colonizing families, non-dispersal probability, and the number of hunting trips – do not influence model outputs at the equilibrium (Table 4, Fig. S1-3). However, the initial number of colonizing families influences the time to reach equilibrium (Fig. S1). The probability of non-dispersal affects the model outputs only during the earlier time steps before the system reaches its stable state, with the number of households larger at the higher non-dispersal rate (Fig. S2).

4.2. Validation

We apply the POM principle (Grimm et al., 2005; see the Method section), which encourages the use of multiple "patterns" found in the dataset rather than trying to calibrate a model to reproduce the exact numbers (Grimm et al., 2005). We have conducted validation with the simulation results for villages 21 and 16 (Fig. 1). We use the same parameter setting as for the sensitivity analysis (Fig. 9), with the 3 ha resolution for both villages.

The results show that a single model can reproduce fairly well the population sizes of the two villages with identical conditions (Fig. 9), except for their locations, land cover and topography. The

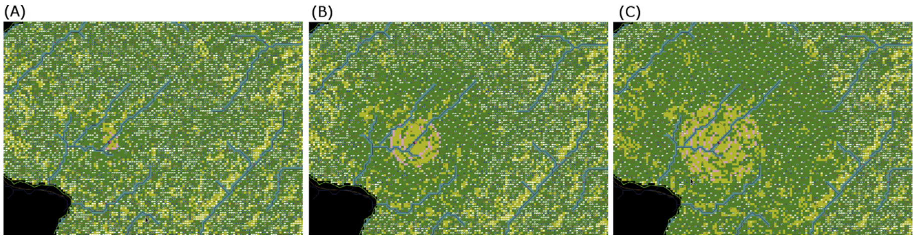

Fig. 4. Expansion of cultivated areas. Snapshots of the simulation at A) 5 years, B) 60 years and C) 160 years since the establishment of a village. The color of the cell represents the type of land cover (green = forest, yellow = grassland, blue = wetland, pink = cultivated area). The village location is represented by the house like icon. Here we use a cell size 8Ha in the simulation. Animal species are represented by different symbols (see the supporting information for the details).

Table 4
Results of sensitivity analyses.

Parameter name	Range	Num. of households	Num. of animals	Species diversity (H)	Carbon loss (%)	Bushmeat ratio (%)	Kill weight (kg)	Hunt distance (km)	Cultivated area (ha)
Cell size (ha)	4–10	35.8–39.0	30340–35200	1.47–1.52	0.26–0.70	77.1–78.2	10.1–10.6	9.5–11.2	0.819–0.823
Hunting success rate (%)	10–40	4.8–48.7	29150–40230	1.47–1.62	0.10–0.72	76.1–88.3	9.6–21.7	9.8–11.4	0.787–0.825
	40–90	42.3–50.6	20220–29150	1.46–1.56	0.72–0.81	75.6–77.1	9.3–9.9	11.2–12.0	0.821–0.827
Fallow periods (yrs)	5–20	32.7–40.8	30520–32370	1.47–1.48	0.39–0.78	0.77–0.78	10.3–10.6	10.4–11.0	0.820–0.822
Prob of non-migration (%)	70–100	35.4–37.5	31660–31790	1.46–1.47	0.52–0.54	0.78–0.78	10.3–10.7	10.4–10.7	0.818–0.821
Hunting trips (n)	8–20	35.8–38.2	31640–32000	1.46–1.48	0.51–0.55	0.78–0.78	10.5–10.6	10.5–10.7	0.819–0.821
Commute range (km)	5–20	29.5–37.1	31610–33250	1.46–1.49	0.43–0.54	0.78–0.80	10.4–11.6	10.1–10.6	0.805–0.820
Number of colonizers	5–15	37.0–37.9	31260–32020	1.47–1.47	0.55–0.56	0.78–0.78	10.3–10.6	10.7–10.7	0.820–0.821

simulations reproduce on average the number of households of Village 21 as 32.8 (*s.d.* = 3.0) while the actual size is 32. Our model simulates the number of households for Village 16 as 47.4 (*s.d.* = 7.5) while the actual number is 47. The simulation results for the size of cultivated areas per household are 0.78 Ha in Village 21 and 0.79 Ha for Village 16. These numbers are within the realistic range of the cultivated areas found in the field data set (0.75 Ha for Village 21, and 0.50 Ha for Village 16). Village 16 actually has an unusually small cultivated area, which we discuss below. While the relative gradient of animal abundance between near (0–6 km range) and far (6–12 km range) may not exactly match the field data, the results capture well the spatial patterns observed in the data for Village 16 and Village 21, where Village 21 has the higher near-far abundance ratio (Fig. 9). The walking distance results indicate that the model reproduces much longer kill distances than the field data, but the relative pattern between the villages is well represented as the households in Village 16 have to walk longer than those in Village 21.

5. Discussion

In this study, we have modeled interactions of social and ecological systems for indigenous peoples and their lands through household-level decision making on hunting and agricultural activities. This model incorporates demographic change, agricultural expansion, wildlife hunting, animal abundance, distribution and diversity, and forest succession based on empirical information (Table 2). Simulation of the establishment of a new village represents interactions between the human population size of a village and the animal population within the village's hunting territory (Figs. 5–8). We have found that, as villages age, the amount of land converted from forest to grassland increases (Fig. 4) and the body mass of killed species decreases, as does species diversity within the hunting territory (Figs. 5–8). In their study of 31 indigenous and colonist settlements ranging from 2 to 25 years since establishment in Neotropical forest, Jerozolimski and Peres (2003) also found that the body size of animals killed by hunters declined as villages become older.

Simulation results have revealed that village population size (represented by the number of households) is the single most important variable in our model. More households means that the amount of deforested areas increases dramatically with crop and fallow lands. Animal diversity and abundance in a hunting territory decline as the number of households increases, due to higher total hunting pressure and habitat fragmentation (Figs. 5–8). Our results show that species with slower population increase rates suffer greater population declines. However, in the simulations, all species persist in the hunting area with the exception of two non-forest species. In our model, a confined hunting territory seems to lead to source-sink metapopulation dynamics around villages when forest cover is maintained. Previous empirical work observed that an increase in human populations in indigenous communities depleted animal populations and resulted in an extension of cultivated areas (Sirén, 2006). Our model confirms this trend, but also suggests that the extent of cultivated areas is indirectly influenced by the availability of natural resources, including animal abundance, through demographic changes.

Simulations of new village formation show that our model successfully predicts the human population size in two different villages when parameterized with field-based data (Fig. 9). This indicates that our model is robust under different situations (Grimm et al., 2005; Windrum et al., 2007). The size of the cultivated area is one of the micro-level variables that we chose to validate. Our simulations have predicted the size of the cultivated area for Village 21 (Fig. 9), but overestimated it for Village 16 (Fig. 9). This may reflect the observation that cassava is harvested in a communal farm in Village 16 unlike other villages in the area. The results indicate that the model predicts realistic spatial patterns of animal abundance (indicated by the ratio of the animal abundance between 0–6 km radius and 6–12 km radius) (Fig. 9).

Process-based simulations can provide useful insights on non-linear events, or so called "surprises", in systems (Verburg et al., 2004). The results of sensitivity analyses on hunting success rate show three "surprises" in the dynamics of our coupled social-ecological system. First, the simulation model is more sensitive to the change in hunting success rate than any other variable we have examined. Secondly, the impact of increase in hunting success rate is more significant when the success rate is low – i.e., this parameter has a non-linear effect. The change in hunting success rate from 10 to 20% causes much difference in the system. Thirdly, the number of households stops increasing when the hunting success rate is greater than 40%, while the animal abundance and diversity are still declining at higher hunting success rates (Fig. 6). This may reflect the negative feedback from declining animal populations as well as a shortage of areas suitable for cultivation for households. Meanwhile the average body mass of killed animals becomes smaller at higher hunting success rates (Fig. 6). Previous studies also showed that higher hunting success rates resulted in lower animal abundance and smaller body size of killed animals (Shepard et al., 2012).

We also found that a shorter fallow period results in higher human populations and animal diversity and abundance (Fig. 7). This is counter-intuitive, as often the larger number of households results in higher hunting pressure and thus should lower animal diversity and abundance. This is because shorter fallow periods can produce more cassava to support a higher human population without the need for expanding the amount of area cultivated, with its associated deforestation and habitat fragmentation. Historically, the productivity of the land decreases with shortened fallow periods, requiring the use of fertilizers or other technological advances, often accompanied by social changes (Boserup, 1965). We have not incorporated these intensification dynamics in the model

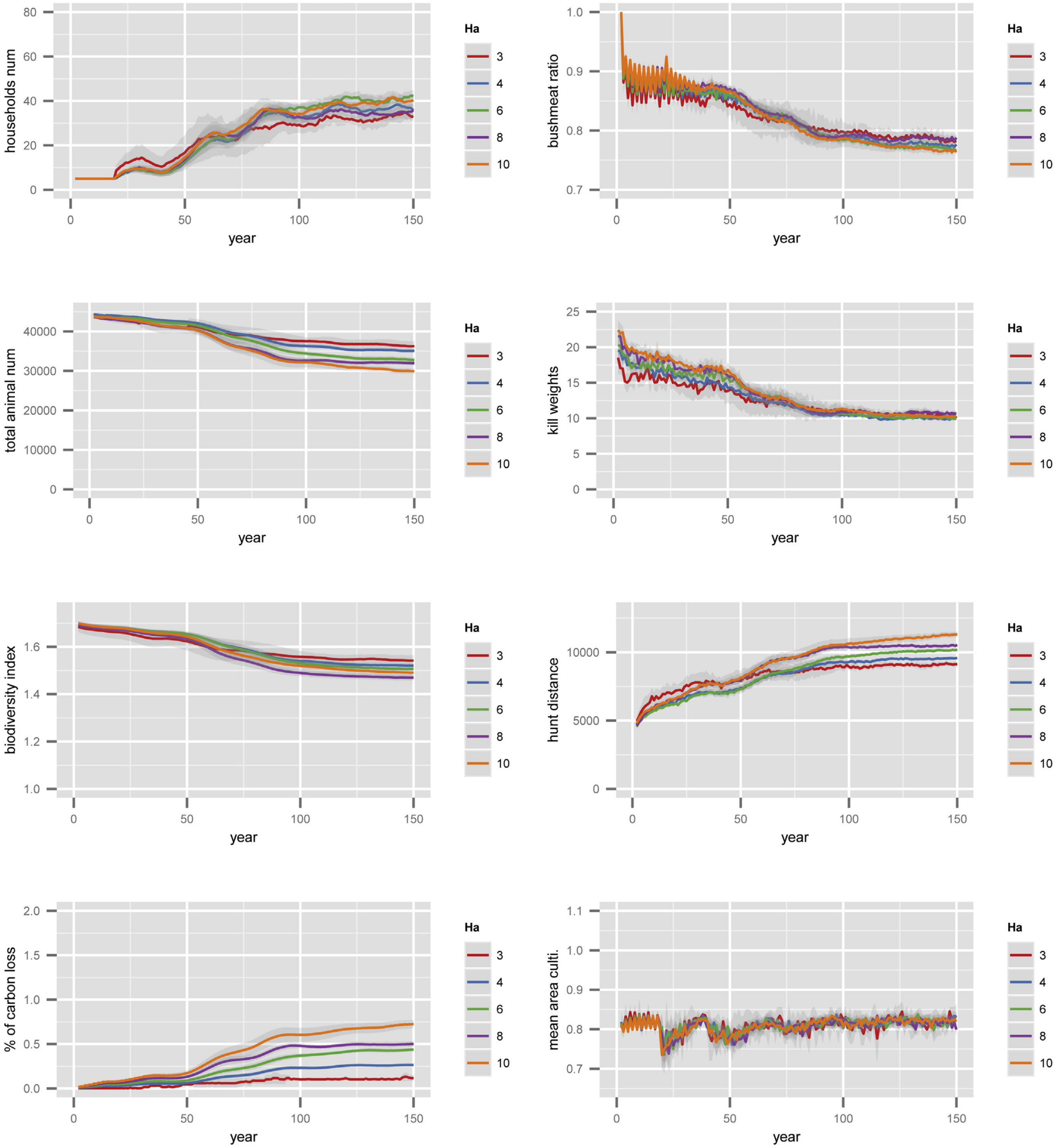

Fig. 5. Sensitivity analysis of the cell size. The *X*-axis represents steps (years) since the start of the simulation. The *Y*-axis represents the number of households ("households num"), the total number of animals in the hunting territory ("total animal num"), biodiversity index measured by the Shannon's H ("biodiversity index"), percentage of carbon loss in the titled land ("% of carbon loss"), ratio of bushmeat consumption to crop consumption ("bushmeat ratio"), the mean distance of kill locations from a village in km ("hunt distance"), the average size of cultivated areas in ha ("mean area culti."), the average weight of the hunted animals in kg ("kill weights"). Colored lines represent the average of 20 simulation runs for different values for the parameter. The gray shadow indicates the 95% confidence interval. Color legends indicate different settings for the sensitivity analysis. We show the results up to 150 years for this analysis, because the computational time at the smallest cell size (3 ha) is too large. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

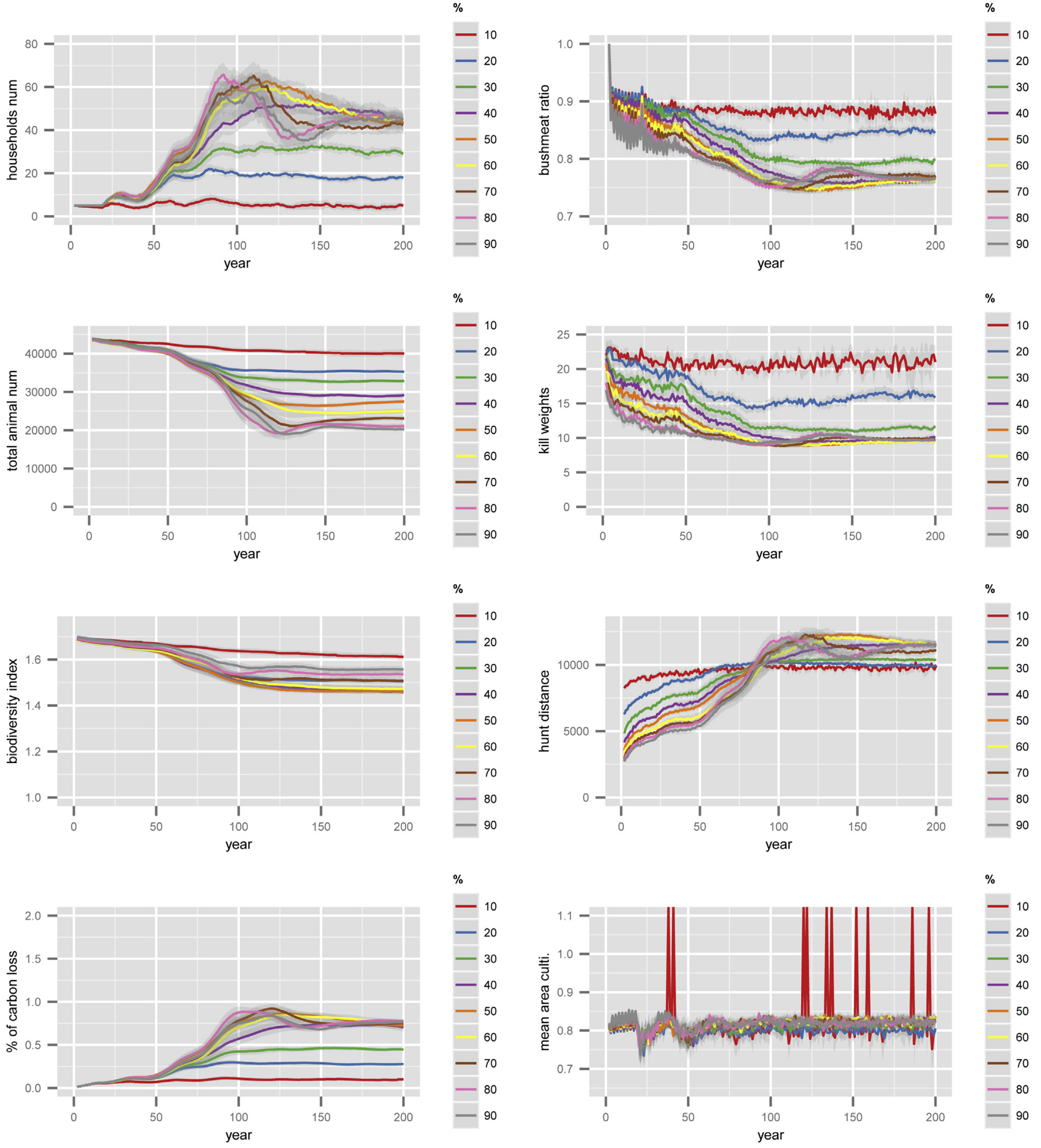

Fig. 6. Sensitivity analysis of the hunting success rate. Same as Fig. 5. We show the results up to 200 years.

as we have not observed this in small villages: households abandon their cropland before it degrades, and clear new areas.

As already suggested by others (Evans and Kelley, 2004), our spatial simulations show that model outputs are sensitive to the choice of cell size (Fig. 5). We chose a 3 ha resolution for the validation because a smaller cell size is computationally too heavy for simulations. In this paper, we introduce our model for the simplest possible conditions and validate it using field data from two remote villages that predominantly rely on wild meat and subsistence farming for sustenance. It is possible to extend our model to incorporate connections with the outside world, such as integration in a market economy, and improvements in health care. Other issues to be analyzed are alternative food resources, such as domestic meat and fish, and other employment opportunities, such as

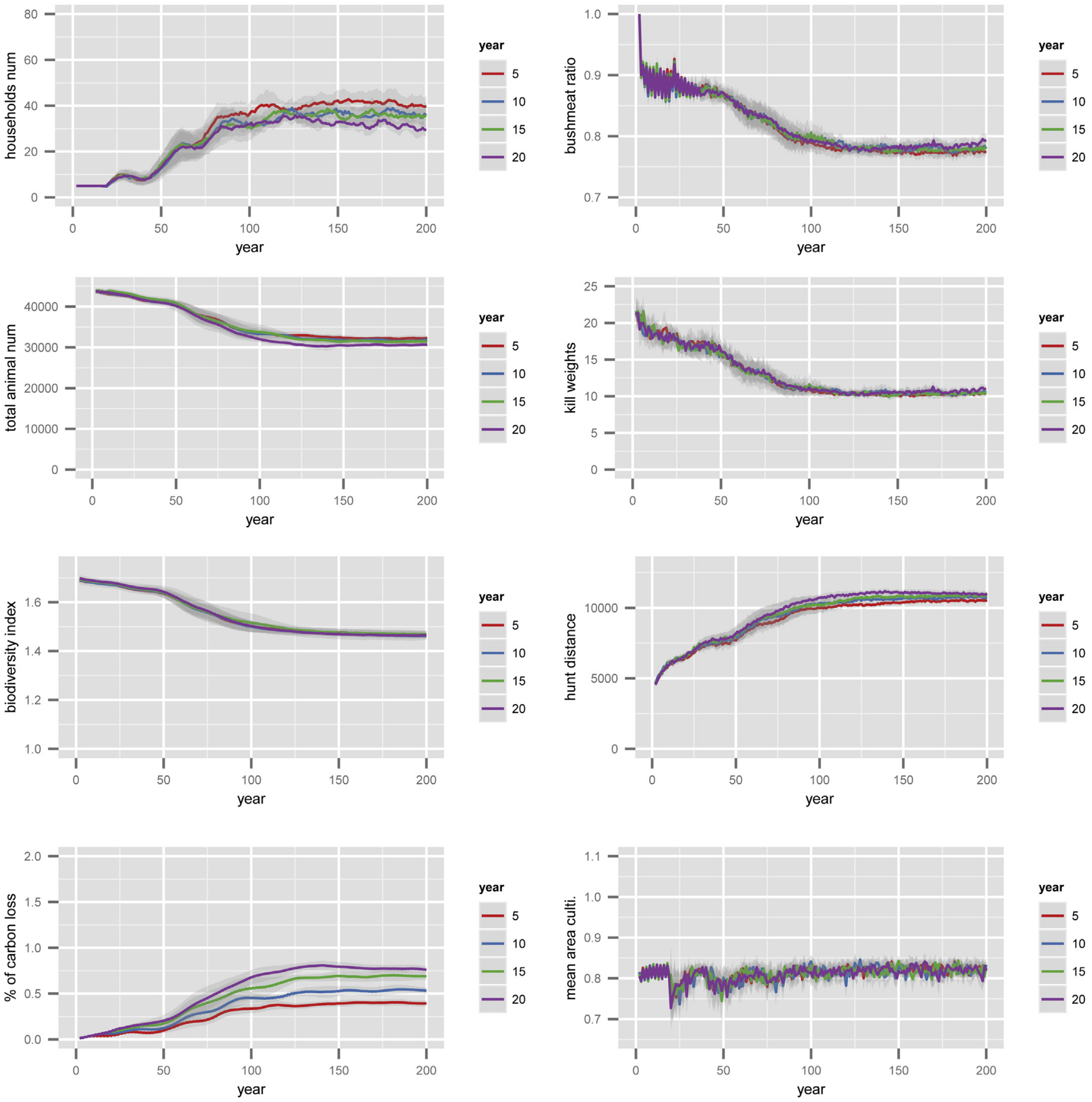

Fig. 7. Sensitivity analysis of the fallow period. Same as Fig. 6.

mining or tourism. Cultural elements significantly affect traditional hunting patterns (e.g., hunting taboos on certain species) in the Rupununi area (Luzar et al., 2012; Luzar and Fragoso, 2013). The model introduced in this paper could be extended to incorporate such elements.

Analyzing interactions and feedbacks between social and ecological systems is critical to understanding the complex pathways of land use change on indigenous lands. In a self-regulating system, equilibrium is achieved through negative feedbacks between the level of human activity and the depletion of natural systems (Berkes and Folke, 1998). In our model, after human population increases to a certain level, animal abundance and diversity show a sudden decline in the hunting territory of a village (Figs. 5–8). With a higher cost of hunting and limited rate of land conversion, the simulation output reaches equilibrium (Figs. 5–8). This suggests that natural resource use by indigenous communities can be sustainable under conditions of limited external influences.

6. Conclusion

Sustainability is best analyzed by examining feedbacks between social and ecological systems (Berkes and Folke, 1998;

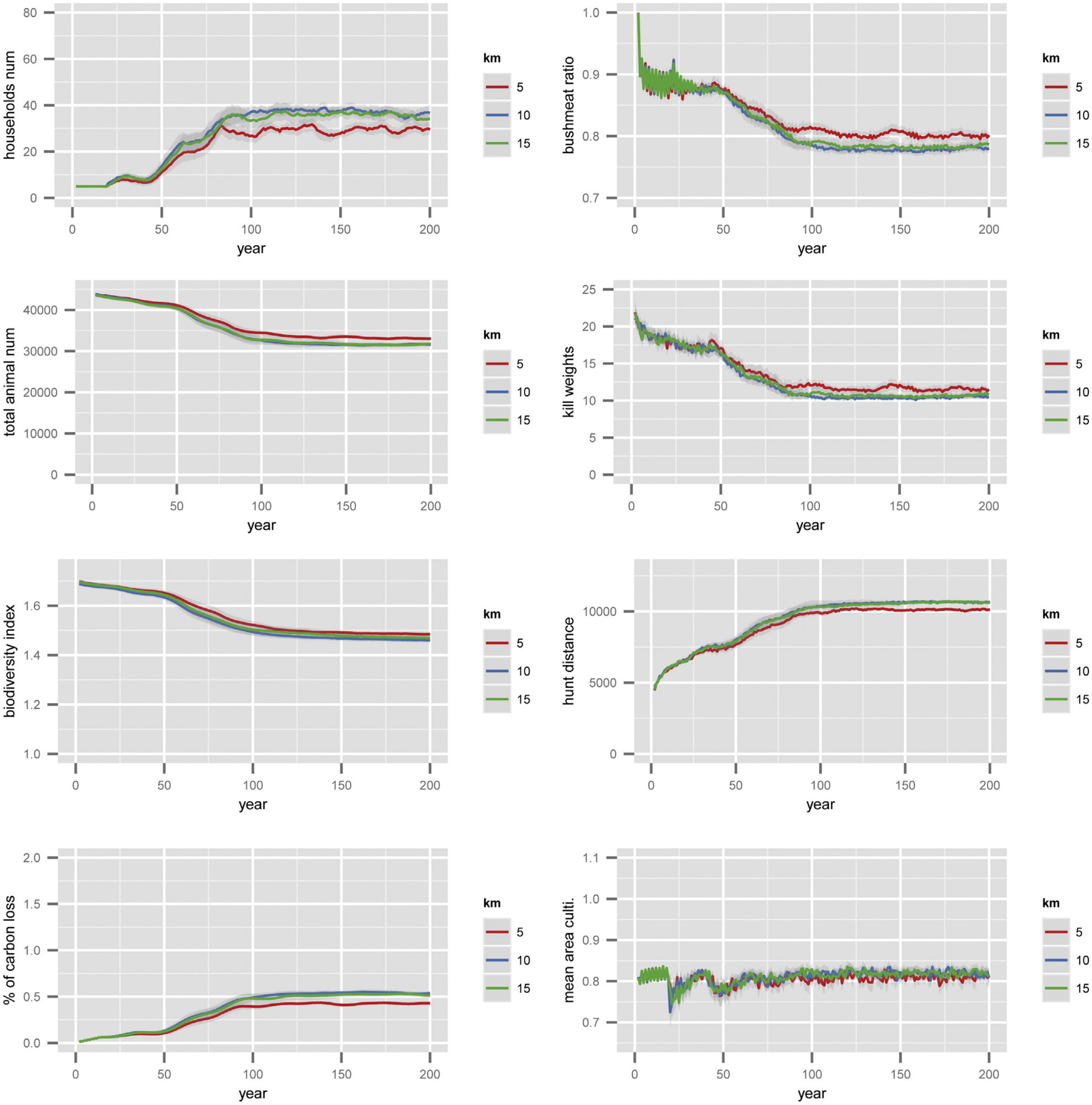

Fig. 8. Sensitivity analysis of the commute distance to cultivated areas. Same as Fig. 6.

Ostrom, 2009; Schluter et al., 2012). In this paper, we describe a simulation model based on rich dataset for indigenous people and their lands in Guyana's Amazon region to examine the dynamics of socio-ecological systems. Our model applies a nutrition model as the decision making mechanism of a household agent in an indigenous territory. Sensitivity analysis shows that simulation results are robust to the wide ranges of unknown parameters, when the model is implemented with the rich dataset from field study, remote sensing and literature. Through simulations of new village formation, our model can estimate the realistic population size for two villages with the same parameter setting, while maintaining other patterns observed in the field. Human population in an indigenous village affects overall environmental conditions in the area, while the maximum size of the human population is largely defined by the availability of resources such as bushmeat and cassava flour. Our model indicates the potential to examine the sustainability of indigenous communities and their lands with a more holistic framework that integrates key feedbacks for maintaining sustainable livelihoods and lands. We believe such a framework contributes to better informed discussions on how to reconcile the preservation of forest cover and biodiversity with human activity.

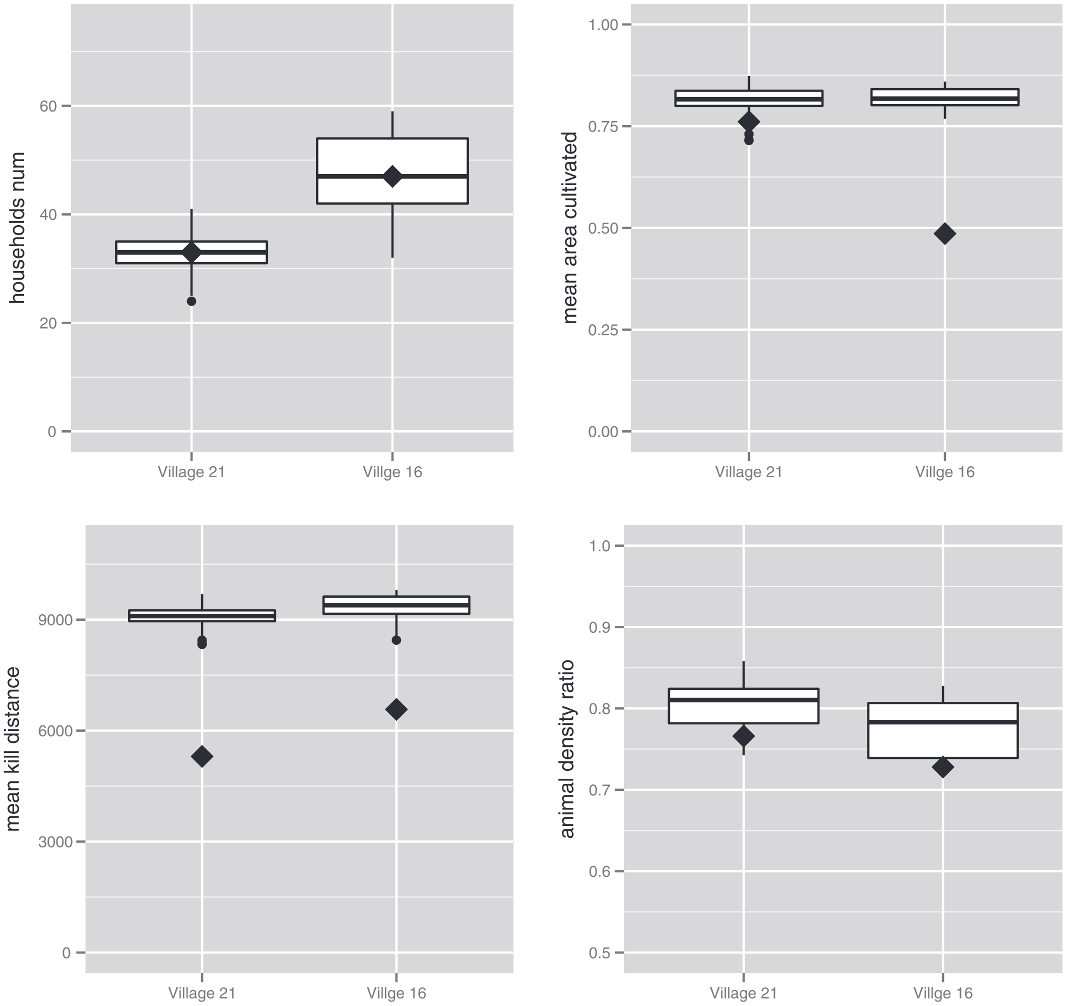

Fig. 9. Validation results. The results of simulations and the actual values for Village 21 and 16 for four different variables; the number of households ("households num"), the average size of cultivated areas in ha ("mean area cultivated"), the mean distance of kill locations from a village in km ("mean hunt distance"), the ratio of animals density in near range (0–6 km) to far range (6–12 km) ("animal density ratio"). Boxplots represent the model outputs at equilibrium (after 80 years) from 20 simulation runs. Simulations were performed until 100 years for each of the experiment ($n = 400$; 20 simulation × 20 years). Square dots represent actual values in these villages.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envsoft.2014.03.008.

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