



Collaborative agent-based modeling for managing shrub encroachment in an Afroalpine grassland

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ABSTRACT

We co-designed an agent-based model of an Afroalpine grassland in Ethiopia that is experiencing unwanted shrub encroachment. The goal was to enable managers of a community conservation area to better understand the drivers of shrub encroachment and to test possible management actions for controlling shrubs. Due to limited site-specific data, we parameterized this model using insights from published literature, remote sensing, and expert opinion from scientists and local managers. We therefore sought to explore potential future scenarios rather than make highly accurate predictions, focusing on facilitating discussions and learning among the diverse co-management team. We evaluated three social-ecological scenarios with our model, examining: (1) the impact of changing precipitation regimes on vegetation, (2) whether changing the frequency of guassa grass harvests would improve the long-term sustainability of the grassland, and (3) whether the combination of grass harvest and shrub removal would affect shrub encroachment. We found that the model was highly sensitive to the amount of grass harvested each year for local use. Our results indicate that the guassa grass was more resilient than shrubs during persistent dry climatic conditions, whereas a reduction in only the early spring rains (known as the “belg”) resulted in considerable loss of grass biomass. While our modeling results lacked the quantitative specificity desired by managers, participants in the collaborative modeling process learned new approaches to planning and management of the conservation area and expanded their knowledge of the ecological complexity of the system. Several participants used the model as a boundary object, interpreting it in ways that reinforced their cultural values and goals for the conservation area. Our work highlights the lack of detailed scientific knowledge of Afroalpine ecosystems, and urges managers to reconnect with traditional ecological management of the conservation area in their pursuit of shrub encroachment solutions. The decline or absence of the belg rains is becoming increasingly common in the Ethiopian highlands, and our results underscore the need for more widespread understanding of how this changing climatic regime impacts local environmental management. This work lays a foundation for social-ecological research to improve both understanding and management of these highly threatened ecosystems.

1. Introduction

Environmental managers are challenged by anticipated future changes and decision-making in the context of limited data and high uncertainty (Polasky et al., 2011). As social-ecological systems continue to change rapidly, the future becomes increasingly uncertain due to the lack of a historical analog and the complex dynamics and feedbacks that

cause unexpected outcomes in these systems (Ostrom, 2007; Liu et al., 2007). In this context, attempts to analyze trade-offs in alternative management practices and decisions require tools that can interweave social and ecological components across diverse spatial and temporal scales (Zimmerer and Basset, 2003; Cumming et al., 2006; Rammer and Seidl, 2015). Spatially-explicit simulation models, such as agent-based models (ABMs), are designed to integrate interactions among agents

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(e.g., people or animals) with landscape-scale processes (e.g., water cycling or vegetation growth) so that their dynamics can give rise to emergent phenomena. This allows ABMs to be effective tools for representing and understanding complex, social-ecological systems in intuitive ways (Janssen, 2005; Barnaud et al., 2008). Agent-based models are also able to mix qualitative, threshold-based rules with quantitative data and mathematical equations (Li et al., 2018), making them particularly useful tools for exploring social-ecological problems when data are limited (Haer et al., 2017; Venkatramanan et al., 2018).

An emerging field of participatory modeling seeks to co-design ABMs with non-academic stakeholders to improve the relevance and utility of the model for decision-making and management (Verburg et al., 2016; Voinov et al., 2018; Schlüter et al., 2019). Part of a growing trend towards knowledge co-production and transdisciplinary science (Norstrom et al., 2020; Molnar and Babai, 2021; Steger et al., 2021c), this collaborative approach combines scientific and societal objectives to advance system understanding as well as collective learning among the diverse people involved in managing a system (Bousquet and Le Page, 2004; Barnaud et al., 2008). Collaborative ABMs are an effective tool for exploring systems in a prospective rather than a purely predictive way (Anselme et al., 2010), which can aid environmental managers in formulating new ideas about how to anticipate and manage systems under future uncertainty. By shifting adaptation planning from reactionary to forward-looking strategies, these collaborative modeling processes can foster complex and long-term thinking, social learning, and collective action (van Notten et al., 2003; Kok et al., 2006), thus improving the adaptive capacity of managers.

Current debates in collaborative ABMs revolve around the level of detail needed for a model to promote this kind of learning among participants. Some scholars insist that highly detailed models are required for decision support, as this allows realistic individual processes to be represented (Barthel et al., 2012) and enables stakeholders to understand how models reflect their everyday, lived experiences (Lange, 2001). However, other scholars have demonstrated that highly realistic models can impede system exploration, leading participants to think in terms of barriers and preventing them from finding innovative solutions (Barnaud et al., 2013). Multiple modeling paradigms have proposed the existence of what we are calling an “intermediate learning hypothesis,” whereby models are most useful for learning and decision-making when they are constructed to reflect intermediate levels of system complexity. Grimm et al. (2005) present a similar concept known as the “Medawar zone”, while members of the Companion Modeling network have described a “KILT: Keep It a Learning Tool” approach (Le Page and Perrotton, 2018). A recent review of 74 dynamic social-ecological models demonstrated that decision support outcomes were highest at intermediate levels of generalizability (Steger et al., 2021b), lending additional support for this hypothesis. Yet few recommendations exist to guide the construction of models at this level of complexity, potentially leading to inconsistent use of this design concept. Our work thus contributes to ongoing conversations regarding the level of model detail that best promotes participant learning in collaborative ABM.

Modeling for decision support and learning is particularly needed in the context of shrub encroachment into grasslands, which has been increasingly observed at variable rates across the globe, resulting in increased density, cover, or biomass of woody plants and the displacement of grasses (Archer et al., 1995; Van Auken, 2009; Eldridge et al., 2011; Sala and Maestre, 2014; Myers-Smith et al., 2015). Changes to ecosystem structure, function, and subsequent goods and services provided by grassland systems makes shrub encroachment an issue of critical concern, particularly for systems that are dependent on livestock production (Sharp et al., 2012; Archer et al., 2017; Martín-Forés et al., 2020). Shrub encroachment is thought to arise from complex, interacting factors such as changing resource availability (e.g., precipitation, soil nutrients, atmospheric CO₂), growing conditions (e.g., microclimate changes, irradiation, topography), and disturbance (e.g., herbivory or the lack thereof, fire, and soil erosion), with the relative influence of

these factors differing according to the particular location (Bestelmeyer et al., 2003; Sankaran et al., 2005; Fuhlendorf et al., 2008; Sankaran et al., 2008; D’Odorico et al., 2012; Lehmann et al., 2014; Midgley and Bond, 2015; Schweiger et al., 2015). While the causes and consequences of shrub encroachment have been examined in the context of arid and semi-arid grasslands (Archer, 1994; Knapp et al., 2008) and temperate mountain ecosystems like the European Alps (Anthelme et al., 2007; Anselme et al., 2010; Komac et al., 2013) and the Tibetan Plateau (Klein et al., 2007; Hopping et al., 2018), little research has been done to understand how these factors play out in wet, tropical mountain systems like Afroalpine grasslands (Buytaert et al., 2011).

In this paper, we describe the process of co-designing an agent-based model of shrub encroachment in a community-managed Afroalpine grassland known as the Guassa Community Conservation Area in the Ethiopian highlands. The purpose of this model is to enable people involved in managing Guassa to explore the individual and combined effects of social and ecological factors controlling the spread of these native shrubs, and to evaluate the efficiency and tradeoffs of different strategies to control their expansion. Due to the scarcity of data from this site, parameter values are derived largely from the literature, remote sensing, and expert opinion from scientists and local managers. While there is some level of realism in the landscape and parameterization, we do not intend to produce highly accurate predictions of the future of this area. Rather, we seek to explore potential futures and use these to facilitate discussion and planning among the diverse co-management team. We assess the learning experienced by participants in the co-design process to contribute to empirical measurements of learning in relation to model complexity.

2. Material and methods

2.1. Study area description

The Guassa Community Conservation Area (Guassa) is 78 km² and located within the Menz Gera woreda (similar to a county) of the Amhara Region of Ethiopia (Fig. 1). Ranging from 2600 to 3560 m. a.s.l., this area is typically characterized by two rainy seasons known as the ‘belg’ (~March 1 – May 30) and ‘kiremt’ (~July 1 – September 30). Guassa supports many endemic and threatened species, including the critically endangered Ethiopian wolf (*Canis simensis*) and the gelada monkey (*Theropithecus gelada*) (Ashenafi et al., 2005). Guassa is named after the guassa grasses (*Festuca macrophylla*) that are culturally and economically valuable to the local communities for their use as thatch, rope, construction material, and forage. In the last 20 years or so, local managers have observed the expansion of three evergreen shrub species: nachillo (*Helichrysum splendidum*), asta (*Erica arborea*), and cheranfi (*Euryops pinifolius*). The nachillo shrubs are of greatest concern to local managers, as they have no locally perceived value for humans or wildlife, and are thought to compete directly with the guassa grasses.

Similar to the European Alps (Anthelme et al., 2007; Anselme et al., 2010; Komac et al., 2013), grass-shrub interactions in the Ethiopian highlands have been regulated by a long history of human activities. Guassa has undergone significant political and land management changes throughout its history (Ashenafi and Leader-Williams, 2005; Steger et al., 2020). The area was managed for hundreds of years (c. 1600–1974) according to the Qero system of communal management that restricted access to the grasses through short (two to three month) open seasons every three to seven years (Ashenafi and Leader-Williams, 2005). The 1975 Agrarian Reform transferred land ownership to the state, leading to a loss of community control and increasingly open access use of the area over the next 17 years (Admassie, 2000; Ashenafi and Leader-Williams, 2005). Community efforts to re-establish exclusive rights to the area were supported by international conservation efforts in the late 1990s, leading to a new co-management regime between local farmers and government agencies (Fischer et al., 2014). In 2012, exclusive use rights to the area were formally restored to the

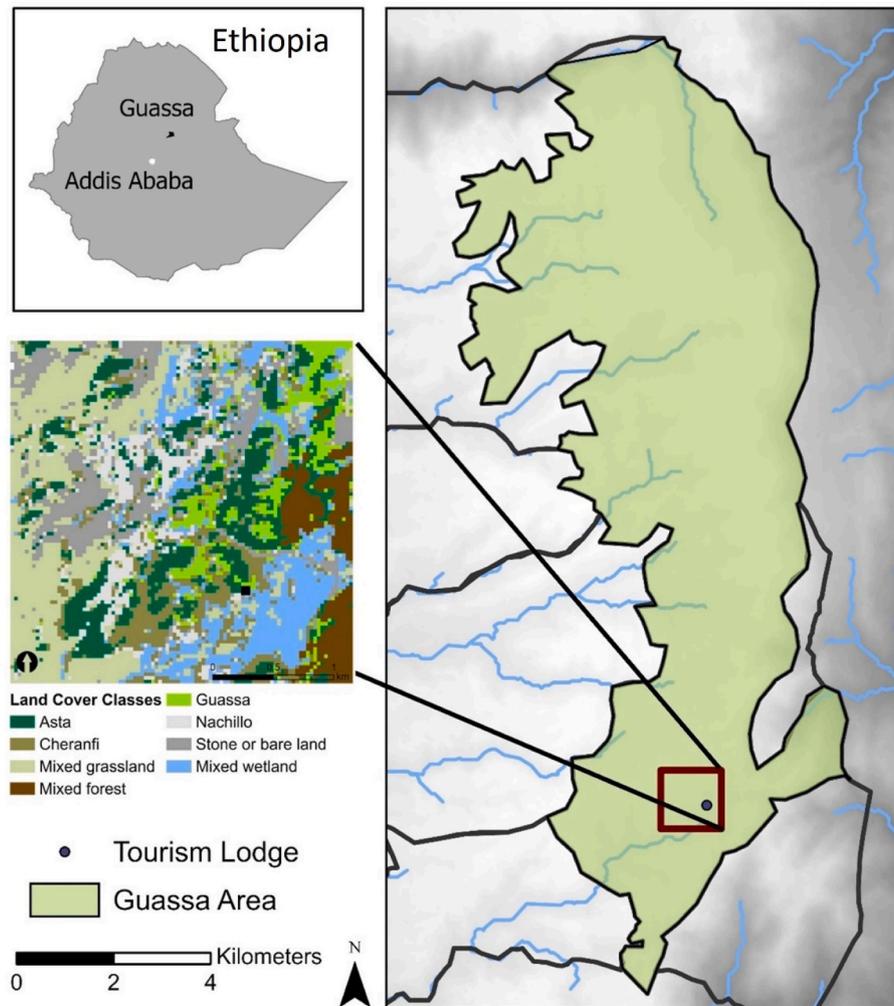


Fig. 1. Map of the Guassa Community Conservation Area. Top left inset map gives the location of the study area in relation to the capital city of Addis Ababa. Lower left inset map focuses on the modeled area.

communities with ancestral rights by Amhara Regional Regulation No. 97.

2.2. Initial model design and Co-design workshops

Local members of the Guassa management team identified shrub encroachment as a critical sustainability concern in the conservation area as part of an on-going collaborative effort to better align scientific research in Guassa with the needs of conservation area managers (Steger et al., 2020). Managers requested that we co-investigate the shrub encroachment issue and test different approaches for removing them nachillo shrubs. An initial ABM was created as a demonstration tool to show managers what kinds of questions can be addressed through simulation modeling. This was a simple version of the final model described in this paper. For example, it modeled guassa grass and nachillo shrubs as individual species but grouped together asta and cheranfi into a mixed shrub category. In August 2019, we convened a workshop to present the initial version of the model with the aim of refining it based on the needs of participants, and generating discussion and learning over its purpose and future application in Guassa. Twenty-eight participants from the Guassa Committee and the Tourism Board, two representatives from the Guassa Conservation office, three Ethiopian and one American scientist, and three officials from the local woreda administration office were in attendance. There were more men ($n = 26$) than women ($n = 11$) present, and the average age of

participants was 40 years. In Sections 2.3 and 2.4 below, we describe some of the co-design decisions made during this workshop before describing the model in detail in section 2.5.

To advance our understanding of whether and how social learning is facilitated through collaborative modeling processes, we assessed the kinds of learning experienced by participants at the workshop. We interviewed each community and stakeholder participant (approximately 15–20 min per person) after the workshop about what they learned from the modeling exercise and discussion, how they anticipate using the model in their management decisions, and whether their understanding of other participants' perspectives changed throughout the workshop. Ethiopian scientists participating in the workshop conducted these interviews in Amharic. Interviews were translated to English and transcribed. The first author used *in vivo* coding (Corbin and Strauss, 2015) and inductive thematic analysis to describe the kinds of learning reported by participants (Boyatzis, 1998).

2.3. Proposed management strategies and climate scenarios

During the workshop, we discussed several potential management options to test with the model. Our aim was to reduce nachillo shrubs and to increase guassa grass provisioning. Managers currently allow guassa grass harvests every three years in May, though in the traditional Qero system they waited as long as five to seven years between harvests (Ashenafi and Leader-Williams, 2005). In recent years, local people have

pushed for more frequent harvesting. Therefore, we tested the impacts of harvesting every two, three, or four years. Based on preliminary fieldwork, scientists originally estimated that each person would not harvest more than 360 kg of guassa grass each harvest (approximately 11 shekims in local measurement units). However, workshop participants described seeing people cut anywhere from 130 to 650 kg (4–20 shekims) in a single day, over multiple if not all the days in the 10-day harvest window (i.e., 1308–6540 kg total). Workshop participants were unable to estimate the average total amount of guassa grass harvested per person, as there has never been a record kept. Therefore, we used the model to estimate a sustainable per person harvest limit for each climate regime in our scenarios to help inform management.

We also discussed the need for mechanical removal of the nachillo shrubs. We aimed to use the model to estimate the intensity and frequency of shrub harvest that would produce the desired reduction (but not elimination) of nachillo shrubs. Local community members identified September as a possible time of year to remove the shrubs, as the long rainy season will have loosened the soil. The systematic removal of these shrubs was not part of the traditional Qero management, though people did often harvest small amounts for firewood. Workshop participants suggested that people would be less motivated to participate in nachillo removal compared to guassa grass harvests, and would thus cut fewer shekims per person. We tested the impact of each person's effort in the shrub removal to find the lowest level of removal per person that would be sufficient to produce the desired outcome, and examined the impacts to vegetation dynamics under different climate regimes.

In total, we evaluated three social-ecological scenarios with our model, comparing them to a co-designed baseline scenario. The baseline scenario reflects a common desired future for the Guassa area where people continue to harvest guassa grasses every three years under an average climate regime. In the first scenario, we explored what would happen under four different climate regimes if the guassa grass harvest was stopped entirely for the next 30 years. These climate regimes include average, wet, and dry precipitation patterns. A fourth climate regime simulates what would happen if the early spring rains do not arrive, which is increasingly occurring in this region (Steger et al., 2020). In the second scenario, we explored how guassa grass harvests would impact vegetation dynamics if they were conducted more (every two years) or less (every four years) frequently than the baseline, and how this harvest frequency interacts with climate. Finally, we explored how the addition of nachillo shrub removal impacted vegetation dynamics across climate regimes, while maintaining the baseline guassa harvest every three years. We simulated 30 iterations of each scenario out to 30 years. Longer timeframes (25 years +) are common in simulation modeling to inform land management (Le et al., 2012; Huber et al., 2013), despite psychological research showing that people have difficulty imagining the future beyond 15–20 years (Boschetti et al., 2015). Previous research with this management team showed that scenario planning and mental modeling processes encouraged managers to extend the time frame they use to think about the Guassa area from five years to twenty (Steger et al., 2021a), which may have prepared them for discussing modeling results this far into the future.

2.4. Strategies and factors not included

Disturbance is a key mechanism of shrub encroachment, yet we decided not to include certain sources of disturbance (i.e., fire, firewood collection, and grazing) at the request of our local collaborators. Under the traditional Qero system, the Guassa area was managed as both a key resource area for livestock grazing as well as a source of guassa grass. When the Qero system was dissolved, the area experienced heavy, uncontrolled grazing and firewood collection which resulted in perceived degradation from 1974 to 2003. Managers banned grazing and firewood collection in 2010 due to concerns over how these activities would impact the future sustainability of the guassa grass and the endangered Ethiopian wolf. Furthermore, fire has never been used as a management

tool in the Guassa area, and in fact it is considered a major threat to the sustainability of the area (Steger et al., 2020), which differs from other regions and ecosystems in Ethiopia (Jacobs and Schloeder, 2002; Gil-Romera et al., 2019). Therefore, we do not include grazing, firewood collection, or fire in our model as potential management options, though we suspect that shrub encroachment has been influenced to some degree by the combined effects of decreased grazing by large animals (cattle, sheep), increased grazing by small animals (rodents), and potentially other yet-unknown dynamics of resource competition.

While our model incorporates some disturbance mechanisms for controlling shrub encroachment (i.e., guassa harvests and shrub removal), we were unable to include potential impacts from other sources due to the lack of available data. For example, impacts from changes to the microclimate (amelioration effects) are likely to exist (Anthelme et al., 2014; Duchicela et al., 2021). Studies of *Helichrysum* spp. and *Festuca* spp. in South Africa showed that *Helichrysum* positively impacts the growth of other species without benefiting *Festuca* as well, which is an indication of strong below-ground competition between the shrubs and grasses (Schweiger et al., 2015). We also remain uncertain as to the potential impacts of increasing atmospheric CO₂ (Bond et al., 2003; Körner, 2006; Archer et al., 2017), and encourage future research into this important issue as it could be having synergistic effects on shrub growth along with observed changes in disturbance regimes.

2.5. Model description

The virtual world of the model consists of 95 x 95 cells, each 30m x 30m, which together represent an 812 ha landscape (Fig. 2). We used the ABM software Netlogo to produce this model (Wilensky, 1999). One time step represented one week in the virtual world. The landscape was modeled after the area surrounding the Guassa lodge, as this is a highly visited and well-known landscape for all managers (Fig. 2). We used a supervised random forest classifier of a February 2019 Landsat 8 image to produce a baseline distribution of the dominant vegetation types in this area, with an overall accuracy of 77.6% (Supplementary Materials). The eight dominant vegetation types are: asta shrubs (*Erica arborea*), cheranfi shrubs (*Euryops pinifolius*), grassland/shrub mix (excluding our target species), guassa grasses (*Festuca macrophylla*), nachillo shrubs (*Helichrysum splendidum*), forest (primarily *Eucalyptus globulus* and *Cupressus lusitanica*), stone, and wetlands (primarily *Carex* and *Cyperus* species). Forests, stone, and wetlands were kept constant in the virtual world; they do not spread and they are unable to be invaded. Previous work in this area indicates that these land cover types do not change rapidly inside the conservation area (Steger et al., 2020), and furthermore are largely unsuitable habitat for the species of interest. The grassland/shrub mix also does not spread, but it is able to be invaded by the four vegetation types that do: guassa grasses, nachillo shrubs, asta shrubs, and cheranfi shrubs. We initialized patches containing these four vegetation types so that each cell contains some biomass (kg/m²) of each type, following a random normal distribution. For example, cells dominated by asta shrubs contain a mean of 0.5 kg asta shrubs with a standard deviation of 0.2 kg, with a mean and SD of 0.1 kg for the three other species. The model begins each timestep by updating the amount of precipitation and associated carrying capacity for each vegetation type, followed by vegetation growth, reproduction, spread, senescence, and harvest. A detailed accounting of the Overview, Design concepts, and Details (ODD protocol; Grimm et al., 2010) for the model is presented in the Supplementary Materials, alongside our code, sensitivity analysis, and a modeler positionality statement aimed at improving equity in agent-based modeling (Williams et al. in review).

2.5.1. Precipitation patterns

We used the Climate Hazards group Infrared Precipitation with Stations data (CHIRPS; Funk et al., 2015), processed through the Climate Engine Application (climateengine.org), to understand past precipitation patterns over Guassa, stretching from 1981 to 2018

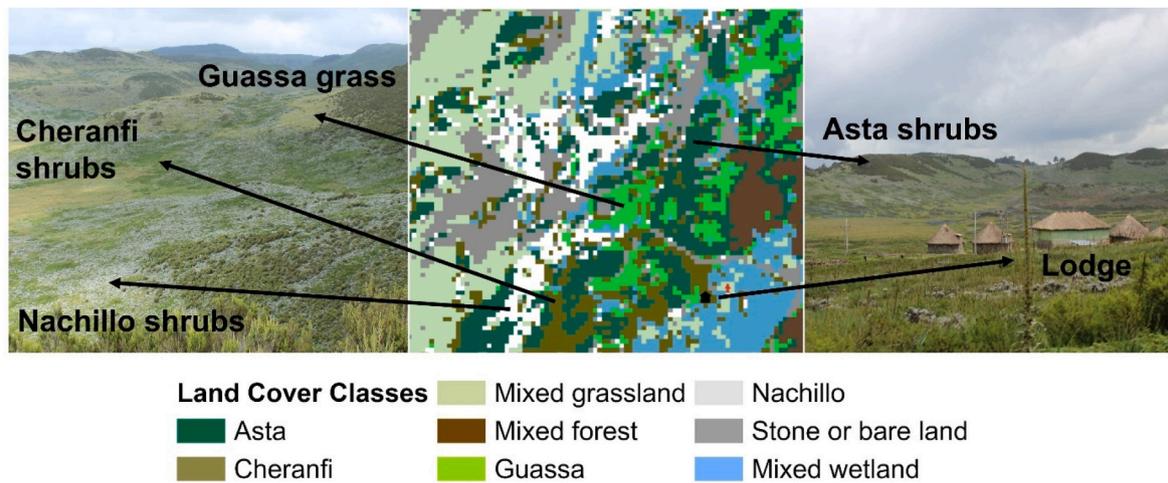


Fig. 2. Guassa grasses (bright green), nachillo shrubs (white), asta shrubs (dark green), and cheranfi shrubs (olive green) are the dynamic plant communities in this model. Forest (brown), stone (grey), and wetlands (blue) do not change. Other mixed grasslands (sage green) do not grow or expand but are able to be invaded by the four dynamic communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Figure S9, Supplementary Materials). CHIRPS data integrates 0.05° resolution satellite imagery with available in-situ station data to produce a gridded time series product that estimates precipitation every day. In conjunction with these historical patterns, we used a published measurement of average annual precipitation from a private climate station in the Guassa area (Fashing et al., 2014). We drew on these data to identify realistic and stochastic patterns of precipitation for our future trends. We estimated average annual precipitation for normal (1600 mm ± 200 mm), wet (1900 mm ± 200 mm) and dry (1300 mm ± 200 mm) climate regimes. Annual precipitation in a year where the early season rains do not arrive (i.e., a “No Belg” climate regime) was about 24% lower than a normal year and changes are concentrated in the belg rainy season of March–May. The dry, average, and wet trends follow the bi-modal seasonal distribution that is historically common throughout the Ethiopian highlands.

2.5.2. Vegetation growth

We estimated carrying capacity for each of the four spreading vegetation types in our model. Data from 2008 provides an above ground biomass estimate for the Guassa area of 480.38 g/m² (no variance reported), with most plots dominated by herbaceous ground covers and guassa grass (Wodaj et al., 2016). We drew on published literature from other Afroalpine regions to estimate biomass for *Helichrysum*-tussock grass mix (Ensslin et al., 2015), *Euryops* spp. (Anderson et al., 2010), and *Erica* spp. (Ensslin et al., 2015). We used the maximum reported biomass estimates to define the carrying capacity for guassa grasses at 0.8 kg/m² for cheranfi shrubs and nachillo shrubs at 1 kg/m², and for asta shrubs at 1.2 kg/m². Following Fryxell et al. (2005), we linked the carrying capacity of these vegetation types to precipitation using a coefficient (ψ). We divided each carrying capacity by the average weekly precipitation in the Guassa area (24.5 mm), yielding estimates of $\Psi_{\text{guassa grass}} = 0.0327$, $\Psi_{\text{nachillo shrubs}} = 0.0408$, $\Psi_{\text{cheranfi shrubs}} = 0.0408$, and $\Psi_{\text{asta shrubs}} = 0.0490$. In the stochastic simulations, ψ is multiplied by the weekly precipitation.

We represented the growth of our four target vegetation types through individual modified logistic growth equations. We assumed weekly growth rates are at a maximum when vegetation biomass is low, as at the beginning of the rainy season or after a disturbance event (Parsons et al., 2001; Fryxell et al., 2005). Therefore, we included a factor that relates the growth rate to standing biomass and precipitation. We further assumed that competition for resources influences both grass and shrub dynamics, and we modified the logistic growth equation to reflect that total biomass from all species restricts growth dynamics in

each individual species equation (D’Odorico et al., 2012). For example, the growth of guassa grass can be represented:

$$\frac{dB_{\text{guassa}}}{dt} = r_{\text{max}} \times [B_{\text{guassa}} + \psi(R)] \times \left[1 - \frac{B_{\text{guassa}} + B_{\text{Helichrysum}} + B_{\text{Euryops}} + B_{\text{Erica}} + \psi(R)}{2 \times \psi(R)} \right] \quad (1)$$

Where B = dry weight biomass (per species), r_{max} = weekly growth rate (per species), and $\psi(R)$ = carrying capacity multiplied by weekly rainfall. This formula produces nested growth curves with maximum and equilibrium values proportionate to daily rainfall, allowing both the maximum rate of grass growth and the carrying capacity to rise and fall with rainfall patterns (Fryxell et al., 2005). Senescence occurs during the 10 weeks following the end of the kiremt season rains. Each week, guassa grass biomass declines by 8%, resulting in 20% biomass remaining in each cell at the start of the next belg rains. Following expert opinion and observation, we programmed nachillo shrubs to senesce at a rate of 4% per week so that 60% of their biomass remains the following year, cheranfi shrubs retain 80% of their biomass, and asta shrubs retain 90% of their biomass in the following year.

Growth rate estimates were derived from MODIS Net Annual Primary Production (NAPP) and Gross Primary Productivity (GPP) products (MOD17A2/3; Running and Zhao, 2015; ORNL, 2018). First, NAPP was converted from kg carbon (kgC) to biomass by dividing by 0.5 (e.g., 0.67 kgC/m²/0.5 = 1.34 kg/m²). The GPP curves showed maximum growth occurring during the kiremt rainy season, which contains 44.4% of the annual precipitation over a twelve-week period. Given that precipitation is a well-established driver of plant growth in most biomes (O’Connor et al., 2001; Knapp et al., 2002), we assumed that the percent of NAPP during this period was roughly the same as the percent of annual precipitation, yielding a maximum per week growth rate of 0.444*1.34 kg/m²/12 weeks = 0.0496 kg/m²/week. We then divided this maximum growth rate into sections for each vegetation type, assuming that guassa grasses and nachillo shrubs are able to grow faster than cheranfi shrubs (Everson et al., 2009), which can in turn grow faster than asta shrubs (Wubie, 2018). Due to the highly derivative nature of this parameterization, we tested a range of maximum growth rate estimates in a sensitivity analysis before conducting the management scenarios, and selected growth rates that produce biomass and distribution patterns that match local perspectives (Supplementary Materials).

2.5.3. Seed production and dispersal

In the model, seeds from the three shrub species are produced and stored in the seed bank of each cell, and germinate in the coming spring when the belg rains arrive. We assumed the seeds of guassa grasses germinate shortly after being shed in July–August, following evidence from observations of *Festuca arundinacea* and *Festuca bromoides* in other systems (Bartolome, 1979; Grime et al., 2014; Thompson et al., 1997) and preliminary findings that guassa grass seeds are largely absent from the Guassa seed bank (Wubie, 2018). Seed production for each vegetation type occurs as a proportion of the aboveground biomass present in each cell, following studies of reproductive allocation and effort (Reekie and Bazzaz, 1987). We took the average reproductive allocation of three *Festuca* species in the literature (Wilson and Thompson, 1989) to estimate that roughly 11% of standing guassa grass biomass is converted to seeds each year. Because reproductive allocation is generally lower in species with low relative growth rates (Bazzaz et al., 1987), we estimated shrub reproductive allocation will be closer to 8% for cheranfi shrubs and 7% for asta shrubs (Vosse et al., 2008). We selected 9% for nachillo because our sensitivity analysis revealed larger proportions caused guassa grasses to completely outcompete nachillo, which did not match observed patterns on the landscape.

Each seed that germinates contributes a small amount towards the total biomass (0.5 g). Maximum germination rates of asta shrubs are 62% under ideal conditions in the laboratory (Mesléard and Lepart, 1991); we assumed an average 40% germination rate under field conditions. Published data on germination rates for nachillo shrubs, cheranfi shrubs, and guassa grasses do not exist; therefore, we used estimates from other species in the same genera (Table F4). We assumed an average 25% germination rate for nachillo shrubs (Doussi and Thanos, 1997; Brown et al., 2003) and an average 80% germination rate for guassa grasses (Rampton and Ching, 1966; Qiu et al., 2010). Finally, we took the average of three species of *Euryops* from South Africa (Brown et al., 2003) and assumed a 23% germination rate for cheranfi shrubs in Guassa. Our sensitivity analysis indicated that model results are not highly impacted by germination rates. Still, future iterations of this model would benefit from species-specific estimates.

Due to the absence of aerial dispersal structures (Molinier and Muller, 1938), asta seeds do not typically spread more than 14 m from their source plant (Mesléard and Lepart, 1991). Therefore, we assumed 80% of the seeds produced will stay in the same 30m × 30m cell of the model, while 20% will spread to neighboring cells equally. We assumed the same distribution for guassa grass seeds, as some *Festuca* species have been shown to have highly restricted dispersal distances (Rabinowitz and Rapp, 1981). *Helichrysum* species observed in South Africa have parachute-type seeds that are adapted for long distance dispersal by wind (Shiponeni and Milton, 2006). These shrubs have been observed to dominate South African seed banks and become the first shrubs to colonize eroded or overgrazed land, largely due to the papery texture of the seeds and their relative unpalatability (Everson et al., 2009). While we do not know that nachillo seeds resemble these other *Helichrysum* species, we assumed they share similar dispersal capabilities. Therefore, we assumed 30% of the seeds produced will stay in the same cell of the model, while 70% will spread to neighboring cells equally. While we were unable to find cheranfi seed dispersal observations, research from South Africa (Vosse et al., 2008) showed similar *Euryops* spp. and *Helichrysum* spp. seed densities in the soil seedbank. Based on this limited information, we assumed 50% of the cheranfi seeds produced will stay in the same cell of the model, while 50% will spread to neighboring cells.

2.5.4. Dominant vegetation cover and transitions

In week 39 of a simulation (late September), we calculated the biomass dominance in each cell that contained over 0.1 kg/m² total biomass across the four spreading vegetation types. We selected this week because it falls after the majority of ecological functions were simulated in the model (seed production and spreading), yet biomass was still high at the end of the main rainy season. We selected the 0.1 kg/

m² threshold to ensure we did not evaluate cells with only very small concentrations of the species of interest. We assumed guassa grasses and nachillo shrubs needed to occupy 40% of the total cell biomass to be considered dominant, while asta and cheranfi shrubs needed to occupy 30% of the total cell biomass to be considered dominant. Because asta and cheranfi shrubs are larger, they can produce higher biomass values than guassa grass or nachillo shrubs in the same amount of space. Therefore, we considered a lower percent cover to be equivalent to the same amount of biomass.

3. Results

3.1. Guassa harvest limits and baseline scenario

We combined insights from the co-design process with a sensitivity analysis to determine that the maximum sustainable harvest limit per person was ~270 kg each harvest for no belg climate, ~700 kg each harvest for dry climate, ~900 kg each harvest for average climate, and ~1100 kg each harvest for wet climate (Supplemental Materials). Increasing these limits by even 100–200 kg (just 3–6 shekims) caused drastic declines in guassa grass biomass and distribution over just five to 15 years when harvesting every three years (Figure S7 Supplementary Materials). These declines were more precipitous when harvests were more frequent (every two years), and less severe when harvests were less frequent (every four years).

Under our baseline scenario, average total biomass across the modeled area for guassa grasses was 442 kg/year and the grasses occupied about 7% of the total landscape (Table S3 Supplementary Materials). Each of the 500 agents in our model harvested an average of 7024 kg (~215 shekims) of harvested guassa grass by the end of the 30 years, which equates to about \$712 USD (21,000 birr) using current market rates for a shekim of guassa. Nachillo shrubs had an average total biomass of 890 kg/year and occupied 7% of the landscape at the end of the 30 year baseline scenario. Asta shrubs had an average total biomass of 1147 kg/year and occupied 21% of the landscape, while cheranfi shrubs had an average total biomass of 1000 kg/year and occupied 9% of the landscape.

3.2. Scenario 1: No harvesting

Compared to the baseline scenario, all species had higher biomass in the wet climate and lower biomass in the no belg climate (Fig. 3). Shrubs only performed better than the baseline under the wet climate, whereas guassa grass had higher biomass in the dry and average climates as well. Under the dry climate, guassa grasses appeared to be considerably more resilient than the shrubs, as their biomass remained near baseline while all shrub species had 20–22% lower biomass. In the average climate, guassa grasses increased biomass 28% from the baseline scenario in the absence of regular harvesting, while all shrub species declined slightly (2.3–2.8%). When comparing across climates within scenario 1, we found that asta shrubs did not differ notably across the dry and no belg climate scenarios, but guassa grasses, nachillo, and cheranfi shrubs had lower biomass in the no belg climate compared to the dry climate. This indicates that the timing of rainfall may have a stronger impact on certain species, including the guassa grasses. The lack of harvest did not impact the overall landscape distribution of any species under any climate (Table S3, Supplementary Materials).

3.3. Scenario 2: changing guassa harvest frequency

Compared to the baseline, all species' biomass increased under a wet climate, though guassa performed better than the shrubs when harvesting occurred every four years (S2. d.4, Fig. 3), and worse than the shrubs when harvesting occurred every two years (S2. d.2, Fig. 3). Under an average climate (S2. c), harvesting more frequently reduced guassa biomass by 7% and harvesting less frequently increased guassa biomass

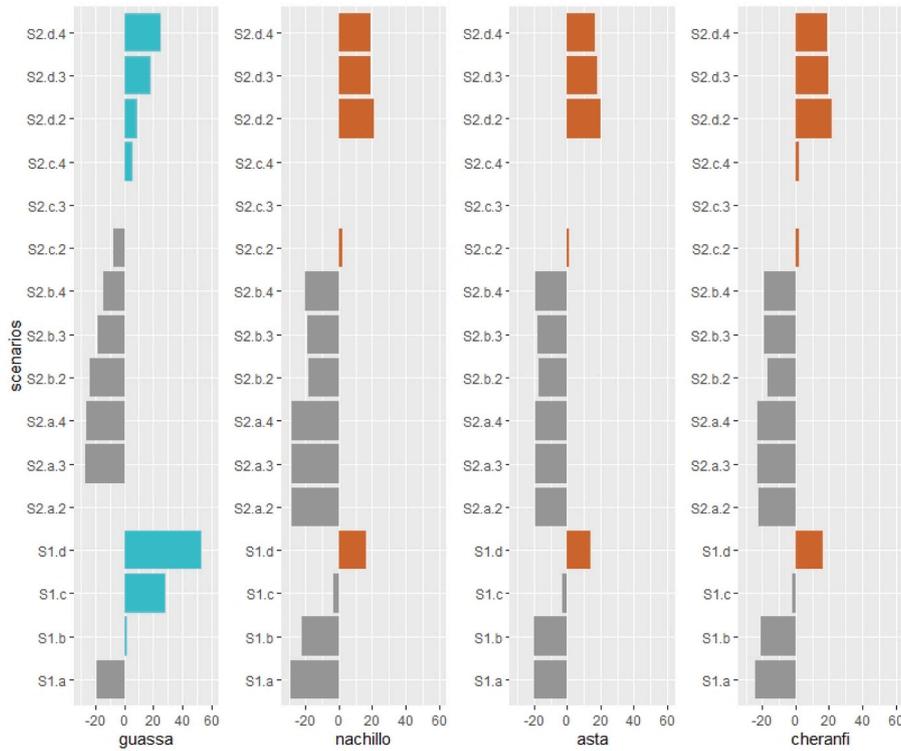


Fig. 3. Percent change in average total biomass per species. S1 = scenario 1 and S2 = scenario 2; a = no belg climate, b = dry climate, c = average climate, d = wet climate; 2 = two year guassa harvest, 3 = three year guassa harvest, 4 = four year guassa harvest. S2. c.3. is the baseline, where average guassa total biomass (across the modeled area) was 442 kg/year, nachillo was 890 kg/year, asta was 1147 kg/year, and cheranfi was 1000 kg/year.

by 6%, while changes to the shrub species were negligible (Fig. 3). Again, the no belg scenario disproportionately impacted guassa grasses and nachillo shrubs, causing a 26–31% decrease in biomass for guassa and a 28% decrease for nachillo across all harvest frequencies, while asta only decreased by 19% and cheranfi by 22–23%.

Harvesting more frequently resulted in higher per person economic benefits, yet harvesting less frequently did not show proportional declines in economic benefits (Fig. 4). For example, harvesting every two years in a wet climate increased per person benefits by \$271, while harvesting every four years decreased them by only \$192 (a difference of \$79). Harvesting guassa every two years under a dry climate produced

the same per person benefit as harvesting every three years in an average climate. However, there appeared to be ecological consequences for guassa grass distribution across the landscape when harvesting more frequently, as guassa distribution decreased to 5% of the landscape and nachillo shrubs expanded to 9% of the landscape under dry, average, and wet climates (Fig. 5, Table F3 Supplementary Materials). Meanwhile, harvesting less frequently did not increase guassa distributions across the landscape, indicating that there may not be proportional ecological benefits to outweigh the economic costs of a less frequent harvest.

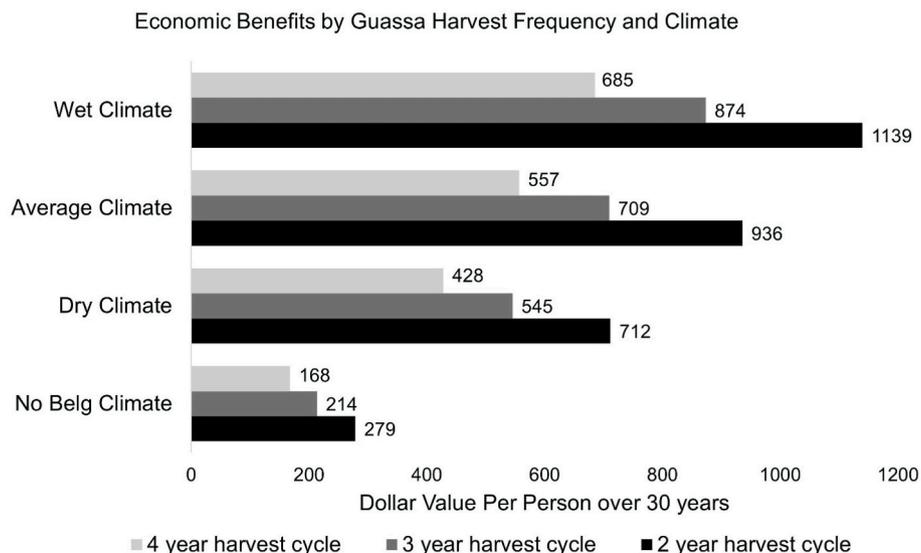


Fig. 4. Per person economic benefits from guassa grass harvest, compared across climate and harvest frequency.

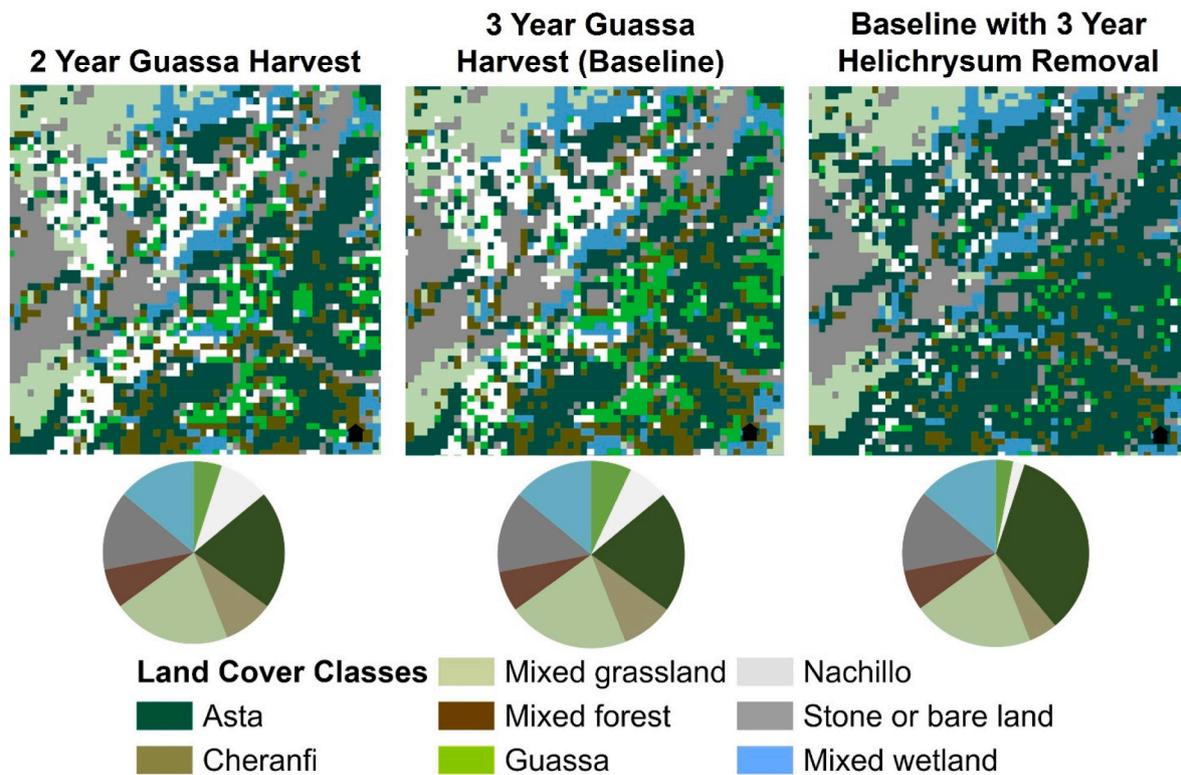


Fig. 5. The baseline scenario (center panel) had guassa grasses and nachillo shrubs each occupying 7% of the landscape. When guassa harvesting increased to every two years (left panel), guassa grass distribution decreased to 5% of the landscape and nachillo shrubs expanded to 9% of the landscape under dry, average, and wet climate regimes. The addition of nachillo removal (right panel) appeared to release competitive control on asta shrubs, which expanded to occupy 34–35% of the landscape, causing range contraction in the three other species of interest.

3.4. Scenario 3: nachillo shrub removal

We found that nachillo shrubs are much more sensitive to removal compared to the guassa grasses; each person only needs to cut an average of 7–11 shekims (250–350 kg) in any climate to observe drastic changes across the landscape. We maintained the baseline guassa harvest frequency of three years across all climates, using the maximum sustainable harvest we determined for each climate. According to workshop participants, the ideal timing for cutting nachillo would be the same year that guassa grasses are harvested, because people would be less likely to illegally harvest guassa during nachillo cutting in this situation. We therefore tested a three-year nachillo removal cycle and found it caused an 8% increase in guassa grass biomass under an average climate compared to the baseline, but did not change average nachillo biomass. This three-year removal cycle mitigated guassa biomass losses in the dry and no belg climates without also benefitting nachillo, and increased guassa biomass in the wet climate by an additional 10% compared to Scenario 2 (with no nachillo removal). However, the nachillo cutting appeared to release competitive control on asta shrubs, which expanded to occupy 34–35% of the landscape – causing range contraction in the three other species of interest (Fig. 5, Table S3 Supplemental Materials). Lengthening the nachillo removal cycle to four years mitigated the range contraction slightly, but many of the benefits to guassa biomass were lost. Increasing the removal cycle to two years had a similar beneficial impact on guassa biomass, but resulted in guassa occupying only 2% of the landscape at the end of the 30 year simulations due to asta shrub expansion (Fig. 5).

3.5. Learning from ABM Co-design

There was evidence that some level of social learning occurred among workshop participants. The ABM itself was made more realistic

as a result of the co-design workshops, which indicates learning accrued by the scientists authoring this paper. The post-workshop interviews ($n = 33$) encouraged participants to reflect on their learning and describe it. The most common theme we found related to the way people saw the model helping them with planning and management of the Guassa area ($n = 23$, 70%), particularly how it could help control the spread of nachillo shrubs ($n = 10$, 30%). Only three people (9%) indicated that the model taught them something specific about the system, such as how harvesting impacts guassa grass growth, or how much each individual should be able to harvest at a time. Four others (12%) explained that the model helped them expand the way they were thinking about options for Guassa management. For example, one man said, “I learned it is possible to plan on the computer about the future of Guassa.” Other people attributed learning to the model when it actually came from conversation around the model. For example, one woman “learned from the model that nachillo has to be removed” while another woman reported that she “learned it is possible to control and manage nachillo” – even though the initial model did not show any nachillo cutting, it merely inspired conversation about the need for cutting. Still others seemed to use the model to reinforce their existing understanding of system management. For example, one man said, “if we protect our guassa, we will always have green guassa.”

Another common theme was how the model helped people see and understand the future ($n = 17$, 51%). This theme occasionally overlapped with the planning and management theme described above, with one priest explaining “It is important to forecast into the future in order to control the Guassa area.” Others emphasized that they would share with people who could not attend the workshop how “it is possible to predict the future of Guassa,” even though the scientist facilitators repeatedly explained that the model was not a true prediction of the future. Four people (12%) seemed to understand this caveat well, as they described the need to put only very high-quality information into the

model to produce good results and see “different possibilities.”

A large subset of people emphasized the ecological insights they gained from the model ($n = 15$, 45%), such as the interactions between nachillo shrubs and guassa grass. Though only a few people mentioned it in their interviews, there was much excitement in our group discussion when the scientists discussed guassa seed production. Most people had never seen guassa seeds before and did not know they existed, possibly because there is no guassa grass cutting allowed during the main rainy season when the grasses set seed. Another subset of people valued the model for the way it displayed the different vegetation types in the conservation area ($n = 13$, 39%), both their distribution and amount across the landscape. This level of realism seemed important for making the model accessible to them; one man explained, “the model matches our understanding.”

4. Discussion

4.1. Social and ecological lessons for guassa management

Overall, our model results support continuing current management of harvesting guassa grasses every three years, as this frequency appears to mitigate negative ecological impacts across climate types while retaining economic benefits for local communities. However, we stress that our model was highly sensitive to changes in guassa harvest amounts. We encourage managers to reflect on climatic conditions in the years surrounding the harvest, as our model identified significantly lower maximum harvest limits during the no belg climate in particular. This is concerning as the loss of early season rains is becoming increasingly common in the Guassa area (Fashing et al., 2014), and across the Ethiopian highlands more broadly (Rosell, 2011; Groth et al., 2020). Experimental studies in temperate grasslands have also shown that delayed or absent spring rains significantly reduced grass seed sprouting and subsequent plant survival (Larson et al., 2021), with potential long-term impacts on species diversity (Stampfli and Zeiter, 2020). More work is needed to understand the impacts of delayed belg rains at both species and community levels.

There are several areas where we seek to expand upon and improve these modeling efforts. For example, our model admittedly treated climate in a simplified way, where each year followed the same seasonal pattern and general precipitation amount. This discrete treatment of climatic conditions was helpful during this initial exploration as it allowed us to isolate the impacts of precipitation patterns in relation to harvest frequency and intensity. A future version of the model that integrates periodic no belg, dry, and wet years into the average climate may help managers identify more consistent harvest amounts and frequencies in the face of a changing climate. Another key area of improvement involves validation, which is notoriously difficult in simulation modeling (Filatova et al., 2013; David et al., 2017). Ideally, we would seek to expand upon our largely qualitative validation process with a quantitative assessment using independent field data. Local data on biological and ecological dynamics in this system would further help us refine our sensitivity analysis to reflect the range of ecologically feasible parameter estimates.

The removal of nachillo shrubs in our model caused an unexpectedly rapid increase of asta shrubs across the conservation area, and a subsequent decrease in the distribution of guassa grasses. However, guassa grass biomass continued to increase despite this range constriction. These results indicate that managers should be cautious of even low-level nachillo removal, and should weigh the benefits and drawbacks of increasing guassa biomass while losing overall landscape cover as a possible unexpected outcome. The loss of landscape cover in the model produced an increased patchiness of the guassa grass community, which may result in decreased patch connectivity and a resultant decline in native plant diversity (Gilbert-Norton et al., 2010). Research on species coexistence through habitat partitioning has demonstrated that differences in dispersal and colonization ability can impact the relative

abundances of species within a community (Levine and Rees, 2002), and that these differences are enabled and constrained based on the patch density and heterogeneity of a habitat (Yu et al., 2001, 2004). More work is needed to understand how habitat heterogeneity interacts with colonization ability to determine the relative abundance of species within communities (Mittelbach and McGill, 2019), and how this plays out in the understudied Afroalpine ecosystem. Our model lays a foundation for this type of ecological inquiry in the Guassa area.

Our inclusion of multiple, interacting shrub species is a novel aspect of the model that is not seen in most spatial shrub encroachment models (Komac et al., 2013; Cao et al., 2019), and which was due in large part to the co-design process, as workshop participants insisted on a certain level of realism in the vegetation patterns seen in the model. In fact, one of the most common types of learning experienced by workshop participants was an improved understanding of how these vegetation types are distributed across the landscape. Yet, workshop participants were more interested in the model for its ability to provide quantitative answers such as the ideal amount of nachillo to cut, how much guassa grass could be harvested at what frequency, and what that meant for the amount of income generated for the community. One local leader ended the co-design process with a very clear statement, “if you tell us how much nachillo to cut, we will cut it.” This statement reflected a high level of trust in the model and scientific process, despite the caveats and cautions presented by scientists throughout the co-design process. Therefore, while this exploratory model has been helpful for scientists thinking about the system, we believe the next iteration of this model needs to be calibrated to locally-collected data to provide more accurate estimations and better meet the needs of local management.

4.2. Insights on Learning Through agent-based models

Social learning requires participants to collectively explore the limits of current knowledge, exchange and generate new knowledge, and understand how this knowledge is situated in a particular socio-cultural context (Keen et al., 2005; Armitage et al., 2011; Baird et al., 2014; Fazey et al., 2014). Despite the integral role that social learning plays in effective knowledge co-production, confusion persists over how to best promote learning via collaborative ABM. We attempted to design our model at an intermediate level of complexity, as this has been suggested to maximize learning (Grimm et al., 2005; Le Page and Perrotton, 2018). However, participants in our co-design process urged increasingly realistic representations in the model, and did not find a qualitative, exploratory use of the model particularly helpful for achieving their management objectives. This pursuit of highly technical, quantitative answers by community members has been observed in other collaborative ABM applications. For example, a Companion Modeling project in Thailand resulted in farmers declaring they would “do as the game showed [them], because then [their] income will increase” (Etienne, 2013). These experiences highlight the potential dangers of collaborative ABM, as misunderstandings and mistranslations may give local participants an incorrect or misleading interpretation of the modeling results. Furthermore, modelers must grapple with the ethical question of engaging in an exploratory modeling process that cannot yield the specific management answers requested by local participants, as they might view their time and effort as wasted.

Although our model was unable to provide specific harvest amounts for guassa and nachillo species, we still found evidence that participants experienced valuable learning throughout the process. Previous research demonstrated that creating and sharing mental models of the Guassa system improved stakeholder relationships among the research team, expanded understanding of the system and its complexities, and extended the time frame Guassa managers use for planning and management (Steger et al., 2021a). In comparison, learning from the ABM specifically seemed to orient more around ecological insights and normative goals for the Guassa area. The model functioned as a boundary object (Steger et al., 2021b) for many of the participants, who

used it to reinforce their current beliefs about the guassa grass importance and the need for control and management of the shrubs. Boundary objects are objects or ideas that emerge through collaboration and dialogue, which have enough interpretive flexibility to adapt to local needs while also fulfilling information needs that apply across more general contexts (Star and Griesemer, 1989; Star, 2010). We believe the model was able to operate as a boundary object for these participants because they interacted with it during the initial co-design period, when the model structure remained quite general. Subsequent workshops were planned to discuss the refined model and the detailed results included in this manuscript, but these workshops were postponed due to the COVID-19 pandemic and ongoing Tigray War. We are therefore unable to provide a more nuanced assessment of participant learning at multiple points throughout a collaborative ABM process, and regret that this has prevented us from validating learning outcomes with participants.

4.3. Knowledge gaps in afroalpine research

Parameterization of this model was hindered by the lack of data available on Afroalpine grassland species. The Afroalpine ecosystem is incredibly diverse, with rare and endemic species often restricted to just one mountaintop or plateau (Gehrke and Linder, 2014; Mairal et al., 2017; Rahbek et al., 2019; Enquist et al., 2019). These species are highly threatened, due primarily to climate change at high altitudes (Pepin et al., 2015) and land use change (Stévant et al., 2019). During our group discussions of the model, scientists repeatedly raised the issue of lack of available data for more accurate predictions from the model. This motivated strong local support for the establishment of vegetation research plots within the Guassa area, which were initiated in 2020. It is our hope that this research will shed light on the ecological mechanisms impacting shrub encroachment in the Guassa area, and provide more concrete guidance for management.

In light of these data gaps, we hope to rekindle trust and appreciation for local knowledge and connect current Guassa management with the details of the traditional Qero system of Guassa management (Ashenafi and Leader-Williams, 2005). For example, we know that much of the Guassa area occurs within what is known as the “ericaceous belt” of the Afroalpine, which can extend roughly from 2600 m to 4100 m (Hedberg, 1951) though is more commonly observed between 3000 m–3200 m in Ethiopia (Friis et al., 2010). The rapid expansion of *asta* shrubs in one modeled scenario indicates that these shrubs have a competitive advantage in this area, and that past human activity was likely critical for maintaining the existence of guassa grass in the ericaceous belt. Firewood harvest of *asta* shrubs was banned in Guassa in 2010 due to possible negative impacts to rodent populations, which account for more than 80% of the diet of the endangered Ethiopian wolf (Ashenafi et al., 2005). Research showed that while total rodent populations were unaffected by firewood harvest, the proportion of wolves’ preferred prey species, the Abyssinian grass rat (*Arvicanthis abyssinicus*), was lower where firewood harvesting occurred (Ashenafi et al., 2012). However, the method of removal and shrub species are important to consider, as *cheranfi* shrubs are often uprooted completely, leaving open areas that may be less desirable habitat for rodents (Ashenafi et al., 2012). Selective and careful cutting of *asta* shrubs in addition to *nachillo* shrubs may present a viable management option for controlling unexpected shrub expansion, which may mitigate negative consequences for rodent populations and which would have additional economic benefits for local people. However, this would require additional investigation, ideally through experimentation in the research plots mentioned above.

Managing shrub encroachment through controlled burning and grazing activity is another critical consideration for future research in the Guassa area. In November 2021, a battle was fought for control of Mehal Meda that resulted in a fire burning over 500 ha of the Guassa area. We intend to assess the impacts of this fire on the vegetation community, and to use this event to discuss with Guassa managers how fire is used in other areas of Ethiopia as a management tool. While there

is no historical analog for fire as a management tool in the Qero system, there is some support for grazing as a sustainable shrub encroachment control from both traditional and scientific perspectives. A 2012 study revealed that Abyssinian grass rat populations were higher in previously grazed areas compared to ungrazed areas in Guassa (Ashenafi et al., 2012), while enclosure experiments in the Bale Mountains revealed no change to rodent populations following livestock removal (Vial et al., 2011). Enclosure experiments to study livestock grazing impacts in Guassa are unlikely in the short term as these are time and resource intensive studies that would require enthusiastic support from managers. We intended to discuss these possibilities with Guassa managers during a subsequent workshop, which was postponed due to the COVID-19 pandemic and ongoing Tigray War.

5. Conclusions

Our research lays a foundation for improved understanding of social-ecological drivers of change in threatened Afroalpine grassland ecosystems, and demonstrates the utility of a collaborative ABM approach to managing shrub encroachment in these ecosystems. Limited data availability required us to parameterize our model using data from other Afroalpine mountain regions as well as the South American paramo, which produced modeling results without the quantitative specificity preferred by managers in Guassa. However, participants still experienced valuable learning from the collaborative modeling and co-design process, though it was at a more general level than was desired by managers. Our model did provide indications that Guassa managers should remain cautious when considering changes to guassa grass harvest amounts and frequency, particularly as climate change (in the form of absent spring rains) exacerbated negative impacts to the grasses. Mechanical removal of *nachillo* shrubs was also contraindicated by the model, which inspired the establishment of vegetation plots to test shrub removal before any widespread application was implemented. We encourage Guassa managers to reconnect with traditional ecological management of the Guassa area when considering the problem of shrub encroachment, as it seems likely that additional disturbance from grazing and firewood collection played important roles in the maintenance of the guassa grass community.

Credit author statement

Cara Steger: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Validation; Writing – original draft; Writing – review & editing. **Randall B. Boone:** Conceptualization, Formal analysis; Methodology, Supervision, Validation; Writing – original draft; Writing – review & editing. **Bikila Warkineh Dullo:** Data curation; Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **Paul Evangelista:** Conceptualization, Formal analysis; Funding acquisition; Methodology, Supervision, Writing – review & editing. **Shambel Alemu:** Data curation, Investigation; Writing – review & editing. **Kflay Gebrehiwot:** Data curation, Investigation; Writing – review & editing. **Julia A. Klein:** Conceptualization, Funding acquisition; Methodology, Supervision, Writing – original draft; Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115040>.

References

- Admassie, Y., 2000. Twenty Years to Nowhere. Property Rights, Land Management and Conservation in Ethiopia. Red Sea Press, Trenton, New Jersey, USA.
- Anderson, P.M.L., Hoffman, M.T., O'Farrell, P.J., 2010. Above ground perennial plant biomass across an altitudinal and land-use gradient in Namaqualand, South Africa. *South Afr. J. Bot.* 76 (3), 471–481.
- Anselme, B., Bousquet, F., Lyet, A., Etienne, M., Fady, B., Le Page, C., 2010. Modelling of spatial dynamics and biodiversity conservation on Lure mountain (France). *Environ. Model. Software* 25 (11), 1385–1398.
- Anthelme, F., Cavieres, L.A., Dangles, O., 2014. Facilitation among plants in alpine environments in the face of climate change. *Front. Plant Sci.* 5, 387. <https://doi.org/10.3389/fpls.2014.00387>.
- Anthelme, F., Villaret, J.-C., Brun, J.-J., 2007. Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale. *J. Veg. Sci.* 18 (3), 355–362.
- Archer, S., 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Vavra, M., Laycock, W., Pieper, R. (Eds.), *Ecological Implications of Livestock Herbivory in the West*. Society for Range Management, Denver, pp. 13–68.
- Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., Woods, S.R., 2017. Woody plant encroachment: causes and consequences. In: *Rangeland Systems*. Springer, Cham, pp. 25–84.
- Archer, S., Schimel, D.S., Holland, E.A., 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* 29 (1), 91–99.
- Armitage, D., Berkes, F., Dale, A., Kocho-Schellenberg, E., Patton, E., 2011. Co-management and the co-production of knowledge: learning to adapt in Canada's Arctic. *Global Environ. Change* 21 (3), 995–1004. <https://doi.org/10.1016/j.gloenvcha.2011.04.006>.
- Ashenafi, Z.T., Leader-Williams, N., 2005. Indigenous common property resource management in the central highlands of Ethiopia. *Hum. Ecol.* 33 (4), 539–563. <https://doi.org/10.1007/s10745-005-5159-9>.
- Ashenafi, Z.T., Coulson, T., Sillero-Zubiri, C., Leader-Williams, N., 2005b. Behaviour and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas. *Anim. Conserv.* 8 (2), 113–121. <https://doi.org/10.1017/S1367943005001952>.
- Ashenafi, Z.T., Leader-Williams, N., Coulson, T., 2012. Consequences of human land use for an Afro-alpine ecological community in Ethiopia. *Conserv. Soc.* 10 (3), 209–216.
- Baird, J., Plummer, R., Haug, C., Huitema, D., 2014. Learning effects of interactive decision-making processes for climate change adaptation. *Global Environ. Change* 27, 51–63.
- Barnaud, C., Bousquet, F., Trebui, G., 2008. Multi-agent simulations to explore rules for rural credit in a highland farming community of Northern Thailand. *Ecol. Econ.* 66 (4), 615–627.
- Barnaud, C., Le Page, C., Dumrongrojwathana, P., Trébui, G., 2013. Spatial Representations Are Not Neutral: Lessons from a Participatory Agent-Based Modelling Process in a Land-Use Conflict, vol. 45. *Environmental Modelling & Software*, pp. 150–159.
- Barthel, R., Reichenau, T.G., Krimly, T., Dabbert, S., Schneider, K., Mauser, W., 2012. Integrated modeling of global change impacts on agriculture and groundwater resources. *Water Resour. Manag.* 26 (7), 1929–1951.
- Bartolome, J.W., 1979. Germination and seedling establishment in California annual grassland. *J. Ecol.* 67 (1), 273–281.
- Bazzaz, F.A., Chiariello, N.R., Coley, P.D., Pitelka, L.F., 1987. Allocating resources to reproduction and defense. *Bioscience* 37 (1), 58–67.
- Bestelmeyer, B.T., Brown, J.R., Havstad, K.M., Alexander, R., Chavez, G., Herrick, J.E., 2003. Development and use of state-and-transition models for rangelands. *J. Range Manag.* 56 (2), 114–126.
- Bond, W.J., Midgley, G.F., Woodward, F.I., 2003. The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biol.* 9 (7), 973–982.
- Bousquet, F., Le Page, C., 2004. Multi-agent simulations and ecosystem management: a review. *Ecol. Model.* 176 (3), 313–332.
- Boyatzis, R.E., 1998. *Transforming Qualitative Information: Thematic Analysis and Code Development*. SAGE.
- Brown, N.A.C., van Staden, J., Daws, M.I., Johnson, T., 2003. Patterns in the seed germination response to smoke in plants from the Cape Floristic Region, South Africa. *South Afr. J. Bot.* 69 (4), 514–525.
- Buytaert, W., Cuesta-Camacho, F., Tobón, C., 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecol. Biogeogr.* 20 (1), 19–33.
- Cao, X., Liu, Y., Cui, X., Chen, J., Chen, X., 2019. Mechanisms, monitoring and modeling of shrub encroachment into grassland: a review. *Int. J. Digit. Earth* 12 (6), 625–641.
- Corbin, J., Strauss, A., 2015. *Basics of Qualitative Research*. SAGE.
- Cumming, G.S., Cumming, D.H.M., Redman, C.L., 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. *Ecol. Soc.* 11 (1).
- David, N., Fachada, N., Rosa, A.C., 2017. Verifying and validating simulations. In: Edmonds, B., Meyer, R. (Eds.), *Simulating Social Complexity: A Handbook. Understanding Complex Systems*. Springer International Publishing, Cham, pp. 173–204.
- D'Odorico, P., Okin, G.S., Bestelmeyer, B.T., 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology* 5 (5), 520–530.
- Doussi, M.A., Thanos, C.A., 1997. Ecophysiology of seed germination in composites inhabiting fire-prone mediterranean ecosystems. In: Ellis, R.H., Black, M., Murdoch, A.J., Hong, T.D. (Eds.), *Basic and Applied Aspects of Seed Biology: Proceedings of the Fifth International Workshop on Seeds*, Reading, 1995. Springer Netherlands, Dordrecht, pp. 641–649.
- Duchicela, S.A., Cuesta, F., Tovar, C., Muriel, P., Jaramillo, R., Salazar, E. and Pinto, E., Microclimatic warming leads to a decrease in species and growth form diversity: insights from a tropical alpine grassland. *Front. Ecol. Evol.*, p.646.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14 (7), 709–722.
- Enquist, B.J., Feng, X., Boyle, B., Maitner, B., Newman, E.A., Jørgensen, P.M., Roehrdanz, P.R., Thiers, B.M., Burger, J.R., Corlett, R.T., Couvreur, T.L., 2019. The commonness of rarity: global and future distribution of rarity across land plants. *Sci. Adv.* 5 (11), eaz0414.
- Enslin, A., Rutten, G., Pommer, U., Zimmermann, R., Hemp, A., Fischer, M., 2015. Effects of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro. *Ecosphere* 6 (3), art45.
- Everson, T.M., Yeaton, R.I., Everson, C.S., 2009. Seed dynamics of *Themeda triandra* in the montane grasslands of South Africa. *Afr. J. Range Forage Sci.* 26 (1), 19–26.
- Fazey, I., Bunse, L., Msika, J., Pinke, M., Preedy, K., Evelyn, A.C., Lambert, E., Hastings, E., Morris, S., Reed, M.S., 2014. Evaluating knowledge exchange in interdisciplinary and multi-stakeholder research. *Global Environ. Change* 25, 204–220.
- Fashing, P.J., Nguyen, N., Venkataraman, V.V., Kerby, J.T., 2014. Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropit and hominin dietary evolution. *Am. J. Phys. Anthropol.* 155 (1), 1–16. <https://doi.org/10.1002/ajpa.22559>.
- Fischer, A., Wakjira, D.T., Weldesemaet, Y.T., Ashenafi, Z.T., 2014. On the interplay of actors in the co-management of natural resources - a dynamic perspective. *World Dev.* 64, 158–168. <https://doi.org/10.1016/j.worlddev.2014.05.026>.
- Filatova, T., Verburg, P.H., Parker, D.C., Stannard, C.A., 2013. Spatial agent-based models for socio-ecological systems: challenges and prospects. *Environ. Model. Software* 45, 1–7.
- Friis, I.B., Demissew, S., Breugel, P.V., 2010. Atlas of the Potential Vegetation of Ethiopia. Det Kongelige Danske Videnskaberne Selskab.
- Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R.E., Hayden, D.T., Holt, R.D., Abrams, P.A., 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers: landscape scale, heterogeneity and Serengeti grazers. *Ecol. Lett.* 8 (3), 328–335.
- Fuhlendorf, S.D., Archer, S.A., Smeins, F., Engle, D.M., Taylor, C.A., 2008. The combined influence of grazing, fire, and herbaceous productivity on tree-grass interactions. In: Van Auken, O.W. (Ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type*. Springer, New York, NY, pp. 219–238.
- Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., Michaelsen, J., 2015. The climate hazards infrared precipitation with stations-a new environmental record for monitoring extremes. *Sci. Data* 2, 150066. <https://doi.org/10.1038/sdata.2015.66>.
- Gehrke, B., Linder, H.P., 2014. Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Bot.* 124 (2), 165–177.
- Gilbert-Norton, L.Y.N.N.E., Wilson, R., Stevens, J.R., Beard, K.H., 2010. A meta-analytic review of corridor effectiveness. *Conserv. Biol.* 24 (3), 660–668.
- Gil-Romera, G., Adolf, C., Benito, B.M., Bittner, L., Johansson, M.U., Grady, D.A., Lamb, H.F., Lemma, B., Fekadu, M., Glaser, B., Mekonnen, B., 2019. Long-term fire resilience of the ericaceous belt, Bale mountains, Ethiopia. *Biol. Lett.* 15 (7), 20190357.
- Grime, J.P., Hodgson, J.G., Hunt, R., 2014. *Comparative Plant Ecology: A Functional Approach to Common British Species*. Springer.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221 (23), 2760–2768.
- Groth, J., Ide, T., Sakdapolrak, P., Kassa, E., Hermans, K., 2020. Deciphering interwoven drivers of environment-related migration-A multisite case study from the Ethiopian highlands. *Global Environ. Change* 63, 102094.
- Haer, T., Botzen, W.W., de Moel, H., Aerts, J.C., 2017. Integrating household risk mitigation behavior in flood risk analysis: an agent-based model approach. *Risk Anal.* 37 (10), 1977–1992.
- Hedberg, O., 1951. Vegetation belts of the east african mountains. *Sven. Bot. Tidskr.* 45 (1), 141–196.
- Hopping, K.A., Knapp, A.K., Dorji, T., Klein, J.A., 2018. Warming and land use change concurrently erode ecosystem services in Tibet. *Global Change Biol.* 24 (11), 5534–5548.

- Huber, R., Briner, S., Peringer, A., Lauber, S., Seidl, R., Widmer, A., Gillet, F., Buttler, A., Le, Q.B., Hirschi, C., 2013. Modeling social-ecological feedback effects in the implementation of payments for environmental services in pasture-woodlands. *Ecol. Soc.* 18 (2).
- Jacobs, M.J., Schloeder, C.A., 2002. Fire frequency and species associations in perennial grasslands of south-west Ethiopia. *Afr. J. Ecol.* 40 (1), 1–9. <https://doi.org/10.1046/j.0141-6707.2001.00347.x>.
- Janssen, M., 2005. Agent-based modeling. In: Proops, J., Safonov (Eds.), *Modeling in Ecological Economics*. Edward Elgar Publishers, Cheltenham, pp. 155–172.
- Klein, J.A., Harte, J., Zhao, X.-Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan plateau. *Ecol. Appl.* 17 (2), 541–557.
- Keen, M., Brown, V.A., Dyball, R., 2005. *Social Learning in Environmental Management: towards a Sustainable Future*. Routledge.
- Knapp, A.K., Briggs, J.M., Collins, S.L., et al., 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biol.* 14, 615–623.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *science* 298 (5601), 2202–2205.
- Kok, K., Rothman, D.S., Patel, M., 2006. Multi-scale narratives from an IA perspective: Part I. European and Mediterranean scenario development. *Futures* 38 (3), 261–284.
- Komac, B., Kefi, S., Nuche, P., Escós, J., Alados, C.L., 2013. Modeling shrub encroachment in subalpine grasslands under different environmental and management scenarios. *J. Environ. Manag.* 121, 160–169.
- Körner, C., 2006. Plant CO2 responses: an issue of definition, time and resource supply. *New Phytol.* 172 (3), 393–411.
- Lange, E., 2001. The limits of realism: perceptions of virtual landscapes. *Landsc. Urban Plann.* 54 (1), 163–182.
- Larson, J.E., Ebinger, K.R., Suding, K.N., 2021. Water the Odds? Spring Rainfall and Emergence-related Seed Traits Drive Plant Recruitment (Oikos).
- Le, Q.B., Seidl, R., Scholz, R.W., 2012. Feedback Loops and Types of Adaptation in the Modelling of Land-Use Decisions in an Agent-Based Simulation, vol. 27. *Environmental Modelling & Software*, pp. 83–96.
- Le Page, C., Perrotton, A., 2018. KILT: a modelling approach based on participatory agent-based simulation of stylized socio-ecosystems to stimulate social learning with local stakeholders. Pages 156–169. In: Dimuro, G.P., Antunes, L. (Eds.), *Multi-Agent Based Simulation XVIII*. Springer International Publishing, Cham.
- Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfli, J., Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.S., Bond, W.J., 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science* 343 (6170), 548–552.
- Levine, J.M., Rees, M., 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *Am. Nat.* 160 (4), 452–467.
- Li, X., Perry, G.L.W., Brierley, G.J., 2018. A spatial simulation model to assess controls upon grassland degradation on the Qinghai-Tibet Plateau, China. *Appl. Geogr.* 98, 166–176.
- Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., 2007. Complexity of coupled human and natural systems. *science* 317 (5844), 1513–1516.
- Martín-Forés, I., Magro, S., Bravo-Oviedo, A., Alfaro-Sánchez, R., Espelta, J.M., Frei, T., Valdés-Correcher, E., Rodríguez Fernández-Blanco, C., Winkel, G., Gerzabek, G., González-Martínez, S.C., 2020. Spontaneous forest regrowth in South-West Europe: consequences for nature's contributions to people. *People Nat.* 2 (4), 980–994.
- Mairal, M., Sanmartín, I., Herrero, A., Pokorny, L., Vargas, P., Aldasoro, J.J., Alarcón, M., 2017. Geographic barriers and Pleistocene climate change shaped patterns of genetic variation in the Eastern Afrotropical biodiversity hotspot. *Sci. Rep.* 7 (1), 1–13.
- Mesléard, F., Lepart, J., 1991. Germination and seedling dynamics of *arbutus unedo* and *Erica arborea* on corsica. *J. Veg. Sci.* 2 (2), 155–164.
- Midgley, G.F., Bond, W.J., 2015. Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. *Nat. Clim. Change* 5 (9), 823–829.
- Mittelbach, G.G., McGill, B.J., 2019. *Community Ecology*. Oxford University Press.
- Molinier, R., Muller, P., 1938. La dissemination des especes vegetales. *Rev. Gen. Bot.*
- Molnár, Z., Babai, D., 2021. Inviting ecologists to delve deeper into traditional ecological knowledge. *Trends Ecol. Evol.*
- Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Rovolainen, V., Schaepman-Strub, G., Wheeler, J. A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015. Climate sensitivity of shrub growth across the tundra biome. *Nat. Clim. Change* 5 (9), 887–891.
- Norstrom, A.V., Cvitanić, C., Lof, M.F., West, S., Wyborn, C., Balvanera, P., Bednarek, A.T., Bennett, E.M., Biggs, R., de Bremond, A., Campbell, B.M., 2020. Principles for knowledge co-production in sustainability research. *Nat. Sustain.* 3, 182–190.
- O'Connor, T.G., Haines, L.M., Snyman, H.A., 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *J. Ecol.* 89 (5), 850–860.
- ORNL, D.A.A.C., 2018. MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA. <https://doi.org/10.3334/ORNLDAAC/1379>. Accessed July 29, 2019. Subset obtained for MOD17A3H product at 10.3354N,39.79E, time period: 2000-01-01 to 2014-01-01, and subset size: 16.5 x 26.5 km.
- Ostrom, E., 2007. A diagnostic approach for going beyond panaceas. *Proc. Natl. Acad. Sci. Unit. States Am.* 104 (39), 15181–15187. <https://doi.org/10.1073/pnas.0702288104>.
- Parsons, A.J., Schwinning, S., Carrère, P., 2001. Plant growth functions and possible spatial and temporal scaling errors in models of herbivory. *Grass Forage Sci.* 56 (1), 21–34.
- Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Change* 5 (5), 424–430. <https://doi.org/10.1038/nclimate2563>.
- Polasky, S., Carpenter, S.R., Folke, C., Keeler, B., 2011. Decision-making under great uncertainty: environmental management in an era of global change. *Trends Ecol. Evol.* 26 (8), 398–404.
- Qiu, J., Bai, Y., Fu, Y.-B., Wilmschurst, J.F., 2010. Spatial variation in temperature thresholds during seed germination of remnant *Festuca hallii* populations across the Canadian prairie. *Environ. Exp. Bot.* 67 (3), 479–486.
- Rabinowitz, D., Rapp, J.K., 1981. Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *Am. J. Bot.* 68 (5), 616–624.
- Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B.O., Holt, B.G., Morueta-Holme, N., Nogués-Bravo, D., Whittaker, R.J., Fjeldså, J., 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365 (6458), 1108–1113.
- Rammer, W., Seidl, R., 2015. Coupling human and natural systems: simulating adaptive management agents in dynamically changing forest landscapes. *Global Environ. Change* 35, 475–485.
- Rampton, H.H., Ching, T.M., 1966. Longevity and dormancy in seeds of several cool-season grasses and legumes buried in soil 1. *Agron. J.* 58 (2), 220–222.
- Reekie, E.G., Bazzaz, F.A., 1987. Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *Am. Nat.* 129 (6), 907–919.
- Rosell, S., 2011. Regional perspective on rainfall change and variability in the central highlands of Ethiopia, 1978–2007. *Appl. Geogr.* 31 (1), 329–338.
- Running, Q.M., Zhao, M., 2015. MOD17A3H MODIS/terra Net primary production yearly L4 global 500m SIN grid V006. NASA EOSDIS Land Processes DAAC. <https://doi.org/10.5067/MODIS/MOD17A3H.006>.
- Sala, O.E., Maestre, F.T., 2014. Grass-woodland transitions: determinants and consequences for ecosystem functioning and provisioning of services. *J. Ecol.* 102 (6), 1357–1362.
- Sankaran, M., Ratnam, J., Hanan, N., 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecol. Biogeogr.* 17 (2), 236–245.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. *Nature* 438 (7069), 846–849. <https://doi.org/10.1038/nature04070>.
- Schlüter, M., Müller, B., Frank, K., 2019. The potential of models and modeling for social-ecological systems research: the reference frame ModSES. *Ecol. Soc.* 24 (1), art31.
- Schweiger, A.H., Otieno, D.O., Kulunge, S.R., Reineking, B., Tenhunen, J., 2015. The Afro-alpine dwarf shrub *Helichrysum citrispinum* favours understory plants through microclimate amelioration. *Plant Ecol. Divers.* 8 (3), 293–303.
- Sharp, E.A., Spooner, P.G., Millar, J., Briggs, S.V., 2012. Can't see the grass for the trees? Community values and perceptions of tree and shrub encroachment in south-eastern Australia. *Landsc. Urban Plann.* 104 (2), 260–269.
- Stampfli, A., Zeiter, M., 2020. The impact of seed deficiency on productivity and on negative drought effect in semi-natural grassland. *J. Veg. Sci.* 31, 1066–1078.
- Star, S.L., 2010. This is not a boundary object: reflections on the origin of a concept. *Sci. Technol. Hum. Val.* 35, 601–617.
- Star, S.L., Griesemer, J.R., 1989. Institutional ecology, 'translations' and boundary objects: amateurs and professionals in Berkeley's Museum of Vertebrate Zoology, 1907–39. *Soc. Stud. Sci.* 19 (3), 387–420. <https://doi.org/10.1177/030631289019003001>.
- Steger, C., Nigusie, G., Alonzo, M., Warkineh, B., Van Den Hoek, J., Fekadu, M., Evangelista, P.H., Klein, J.A., 2020. Knowledge coproduction improves understanding of environmental change in the Ethiopian highlands. *Ecol. Soc.* 25 (2).
- Steger, C., Gebrehiwot, K., Chengere, S.A., Marinkovich, J., Dullo, B.W., Zewde, S.W., Klein, J.A., 2021a. Mental models of a social-ecological system facilitate social learning among a diverse management team. *Environ. Sci. Pol.* 122, 127–138.
- Steger, C., Hirsch, S., Cosgrove, C., Inman, S., Nost, E., Shinbrot, X., Thorn, J.P., Brown, D.G., Grêt-Regamey, A., Müller, B., Reid, R.S., 2021b. Linking model design and application for transdisciplinary approaches in social-ecological systems. *Global Environ. Change* 66, 102201.
- Steger, C., Klein, J.A., Reid, R.S., Lavorel, S., Tucker, C., Hopping, K.A., Marchant, R., Teel, T., Cuni-Sanchez, A., Dorji, T., Greenwood, G., 2021c. Science with society: evidence-based guidance for best practices in environmental transdisciplinary work. *Global Environ. Change* 68, 102240.
- Stévant, T., Dauby, G., Lowry, P.P., Blach-Overgaard, A., Droissart, V., Harris, D.J., Mackinder, B.A., Schatz, G.E., Sonké, B., Sosef, M.S., Svenning, J.C., 2019. A third of the tropical African flora is potentially threatened with extinction. *Sci. Adv.* 5 (11), eaax9444.
- Thompson, K., Bakker, J.P., Bekker, R.M., 1997. *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press.

- Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *J. Environ. Manag.* 90 (10), 2931–2942.
- van Notten, P.W.F., Rotmans, J., van Asselt, M.B.A., Rothman, D.S., 2003. An updated scenario typology. *Futures* 35 (5), 423–443.
- Venkatramanan, S., Lewis, B., Chen, J., Higdon, D., Vullikanti, A., Marathe, M., 2018. Using data-driven agent-based models for forecasting emerging infectious diseases. *Epidemics* 22, 43–49.
- Verburg, P.H., Dearing, J.A., Dyke, J.G., van der Leeuw, S., Seitzinger, S., Steffen, W., Syvitski, J., 2016. Methods and approaches to modelling the Anthropocene. *Global Environ. Change* 39, 328–340.
- Voinov, A., Jenni, K., Gray, S., Kolagani, N., Glynn, P.D., Bommel, P., Prell, C., Zellner, M., Paolisso, M., Jordan, R., Sterling, E., Schmitt Olabisi, L., Giabbanelli, P. J., Sun, Z., Le Page, C., Elsawah, S., BenDor, T.K., Hubacek, K., Laursen, B.K., Jetter, A., Basco-Carrera, L., Singer, A., Young, L., Brunacini, J., Smajgl, A., 2018. Tools and methods in participatory modeling: selecting the right tool for the job. *Environ. Model. Software* 109, 232–255.
- Vosse, S., Esler, K.J., Richardson, D.M., Holmes, P.M., 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. *South Afr. J. Bot.* 74 (3), 432–444.
- Vial, F., Macdonald, D.W., Haydon, D.T., 2011. Response of endemic afroalpine rodents to the removal of livestock grazing pressure. *Curr. Zool.* 57 (6), 741–750.
- Wilensky, U., 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL. <http://ccl.northwestern.edu/netlogo/>.
- Wilson, A.M., Thompson, K., 1989. A comparative study of reproductive allocation in 40 British grasses. *Funct. Ecol.* 3 (3), 297–302.
- Wodaj, H., Kelbessa, E., Woldu, Z., 2016. Floristic composition and herbaceous aboveground dry weight biomass of afroalpine vegetation in guassa community conservation area, north shewa, Ethiopia. *Int. Res. J. Biol. Sci.* 5 (1), 26–36.
- Wubie, S., 2018. June 5. Factors determining the population structures of *Festuca macrophylla* hochst. Ex A.rich. And *Helichrysum splendidum* (thunb.) less. In: In Guassa Community Conservation Area, Amhara Regional State, Ethiopia. Thesis, Addis Ababa University.
- Yu, D.W., Wilson, H.B., Pierce, N.E., 2001. An empirical model of species coexistence in a spatially structured environment. *Ecology* 82 (6), 1761–1771.
- Yu, D.W., Wilson, H.B., Frederickson, M.E., Palomino, W., De La Colina, R., Edwards, D. P., Balareso, A.A., 2004. Experimental demonstration of species coexistence enabled by dispersal limitation. *J. Anim. Ecol.* 73 (6), 1102–1114.
- Zimmerer, K.S., Bassett, T.J., 2003. *Political Ecology: an Integrative Approach to Geography and Environment-Development Studies*. Guilford Press.