

# Impacts of Cattle, Hunting, and Natural Gas Development in a Rangeland Ecosystem

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***Abstract.** This paper investigates the impacts from natural gas development, hunting, and cattle grazing on a typical Western U.S. rangeland ecosystem using a general equilibrium model that describes ecosystem dynamics. The study area is located in the region surrounding the Atlantic Rim Natural Gas project in southern-central Wyoming and analyzes the population densities of various species, net hunting benefits, cattle profits, and existence value of sage grouse. The general equilibrium model analyzes the responses of six animal species, two plant species, and accounts for differences in prey scarcity inside and outside the disturbed areas around the wells. The differences in scarcity arise from sage grouse, mule deer, and elk experiencing stress in the disturbed areas and the changes in foraging behavior from the rest of the species. The simulations highlight the advantage of a general equilibrium ecosystem model because it is capable of capturing the complex changes that occur between plant and animal species when natural gas development reduces the habitat of vulnerable species. For the study area, the present-value loss in ecosystem services is \$58.40 million (or \$2,796 per ha), but could vary between -\$0.12 and \$81.67 million depending on the size of the disturbed area and coordination of government agencies.*

**Keywords:** ecosystem modelling, sage brush ecosystem, biodiversity, habitat loss, energy development, ecosystem services.

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## 25 **1 Introduction**

26 Natural gas development (NGD) in the U.S. is proceeding at a rapid pace to meet the  
27 increasing national and international demand for energy needed to fuel economic activities. U.S.  
28 production increased from 23.5 trillion cubic feet (Tcf) in 2005 to 32.5 Tcf in 2016, and the main  
29 reason for this growth was the shale-gas revolution comprising a combination of horizontal drilling  
30 and hydraulic fracturing (Joskow, 2013; Mason and Roberts, 2018). In Colorado and Wyoming, the  
31 two largest producing states in the Intermountain West, the number of natural-gas wells increased  
32 fivefold from the mid-1990s to 2017 (U.S. Energy Information Administration, 2018). While the  
33 benefits of NGD are fairly well understood and measurable (Gillingham and Huang, 2019), as are  
34 the economic costs of procuring the natural gas (Chermak and Patrick, 1995), the costs to  
35 ecosystems that NGD generates are more nebulous and difficult to measure (Naugle 2011, Brady et  
36 al., 2015). These latter costs are a type of externality; that is, a cost external to the marketplace that  
37 negatively impacts people who receive no compensation for their loss. Specifically, in the NGD  
38 case, there are ecosystem externalities (Crocker and Tschirhart 1992) that occur when NGD alters  
39 the equilibrium of an ecosystem and diminishes the ecosystem services provided.

40 The objective of this research is to build an ecological model that quantifies how NGD  
41 impacts important ecosystem services and how economic activities affect each other. The model  
42 tracks over time the populations of seven native species in a sagebrush ecosystem in the  
43 Intermountain West. We choose to focus on three services provided by the ecosystem in the form of  
44 cattle (*Bovidae* Gray, 1821) grazing, existence value of the greater sage-grouse (*Centrocercus*  
45 *urophasianus* Bonaparte, 1827), and hunting of elk (*Cervus elaphus canadensis* Erxleben, 1777),  
46 mule deer (*Odocoileus hemionus* Rafinesque, 1817), and pronghorn (*Antilocapra americana* Ord,  
47 1815). A steady state of this system previous to NGD disturbances is determined based on historic  
48 levels of grazing and hunting. Then NGD is introduced which allows us to estimate changes in the

49 ecosystem services based on how NGD alters the native species populations which, in turn, alters  
50 the grazing and hunting opportunities.

51 While some species will experience immediate habitat loss from NGD, the long-run impacts  
52 on populations will depend on the complex interactions between plant and animal species (Estes et  
53 al., 1998). In the model, these interactions include predator-prey (e.g., elk-grass foraging) and  
54 competitive relationships (e.g., pronghorn and jackrabbits foraging on shrubs) among the native  
55 species, in addition to ungulate competition with cattle. NGD infrastructure includes well pads,  
56 gathering pipelines, roads and structures, although we focus exclusively on areas surrounding well  
57 pads. The impact on species populations is measured in the model by considering their relative  
58 abundance in areas disturbed or undisturbed by NGD. Studies indicate that species such as the sage  
59 grouse, elk, and mule deer avoid natural-gas wells and the areas surrounding them (e.g., Walker et  
60 al., 2007; Doherty et al., 2008). To include this effect, we assume that some species experience  
61 energy losses due to stress from foraging close to the wells. Species' populations are then affected  
62 over time in complicated ways because of differential forage and prey availability between  
63 disturbed areas and undisturbed areas. Our approach tracks how differing changes in prey/forage  
64 availability across areas impacts the accumulation of individual organisms' net energies, biomass  
65 consumptions, predation rates, natural death rates, and birth rates. The combination of these impacts  
66 provides a prediction of how NGD affects an ecosystem and the associated services.

67 Northrup and Wittemyer (2013) reviewed the literature on the ecological ramifications of  
68 the disturbances caused by development of alternative and unconventional sources of energy. They  
69 advocate that "future studies [should] take a comprehensive approach incorporating a mechanistic  
70 understanding of the interplay between development-caused impacts and species ecology that will  
71 enable effective mitigation." (p. 112) This type of comprehensive approach employing an integrated  
72 ecological model is the primary contribution of our paper. Our simulation results show that the

73 introduction of NGD into a rangeland ecosystem generally has negative effects on the population of  
74 some species other than the ones directly affected by NGD, although these effects can be mitigated  
75 to some extent by adjusting the intensity of other human disturbance such as cattle grazing and  
76 hunting.

## 77 78 **2 Materials and Methods**

### 79 **2.1 Study Area**

80 The study area is the Atlantic Rim Natural Gas (ARNG) development project in Carbon  
81 County, Wyoming. The ARNG in the south-central part of the State covers 109,339 ha that is 64%  
82 federal, 31% private, and 5% state owned. ARNG development is within the sagebrush-steppe  
83 ecosystem that covers about 43 million ha in eleven western states and one Canadian province  
84 (Rowland et al., 2010). According to the U.S. Bureau of Land Management (BLM, 2007), the  
85 ARNG is home to 338 recorded species of wildlife, and it provides ecosystem services both to  
86 ranchers who graze cattle on public land managed by BLM, and to elk, mule deer, and pronghorn  
87 hunters. We chose the ARNG because the development represents a large, sudden shock to a  
88 rangeland ecosystem, and the BLM (2007) produced an environmental impact statement (EIS) that  
89 provides an additional source of information regarding the project and relevant ecosystem.

90 The ARNG project develops coalbed methane/natural gas, which is considered an  
91 unconventional form of natural gas that is deposited in coal seams. The natural gas is reached with  
92 vertical and horizontal drilling, and for some wells in ARNG hydraulic fracturing is necessary  
93 (Warren Resources, 2014). The ARNG development started in 1998. It consisted of 627 natural-gas  
94 wells during 2005-2010, but it is scheduled to contain up to 2,000 wells that will be operated by  
95 multiple companies throughout the 30-50 year life of the project (BLM, 2007). Even at historically  
96 low current natural-gas prices, the project is predicted to generate approximately 1.35 trillion ft<sup>3</sup> of

97 natural gas over its lifetime. Annual U.S. consumption of natural gas was about 27 trillion ft<sup>3</sup> in  
98 2017 (BLM, 2007). The ARNG is not only disturbed by NGD; the region is also under constant  
99 pressure from other types of human activities such as transmission lines, roads, and housing (Hanser  
100 et al., 2011, p. 24). However, we focus on NGD because it represents a substantial, relatively  
101 sudden disturbance to the rangeland ecosystem.<sup>1</sup>

102 In 2007, both the National and the Wyoming Wildlife Federations appealed BLM's ARNG  
103 management plan, claiming that the plan did not adequately protect species in the region and  
104 adversely impacts ecosystem services such as hunting, fishing, and wildlife viewing (NWF, 2007).  
105 The appeal was dismissed, although in 2012 both groups again appealed claiming BLM did not  
106 consider new environmental information and impacts on recreational opportunities. The outcome of  
107 this appeal is pending (Warren Resources, 2014).

108

## 109 **2.2 Ecological Model**

110 The food web for ARNG is limited to seven native species and one non-native species  
111 (cattle) as shown in Figure 1. There are two trophic levels, with two plants comprising the first  
112 trophic level and six herbivores the second.

113 The relationships in the food web are modeled using the general equilibrium ecosystem  
114 model (GEEM, Tschirhart 2000). The basic premise behind GEEM is that ecosystem properties,  
115 and species' populations in particular, are ultimately determined by individual organisms'  
116 behaviors; therefore, population-updating equations should be derived from individual behaviors.  
117 GEEM accomplishes this by assuming species' individuals are energy optimizers, similar to optimal

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<sup>1</sup> NGD affects species in different ways. For example, roads built because of natural-gas extraction affect sage grouse more directly. Declines in lek attendance were positively correlated with vehicle traffic levels, and vehicular activity during the daily strutting period on roads within 1.3km of a lek. Reducing overall traffic volumes and isolating traffic disturbance within gas fields could reduce road effects (Holloran, 2005).

118 foraging theory, and the results of the optimization problems are used to construct population-  
119 updating equations. Abrams (1999) pointed out that most studies employing optimum foraging  
120 ignore population dynamics, and most studies of population dynamics ignore optimum foraging.  
121 GEEM is an attempt to bridge the gap by showing that multiple optimal foragers can interact in a  
122 single model that yields reasonable and consistent results. (For other applications of GEEM see  
123 Finnoff and Tschirhart, 2009; Kim et al., 2007; Tschirhart, 2004).

124         The GEEM has four main components: individuals' net energy functions ( $R$ ); first-order  
125 conditions for maximizing net energy (FOCs); predator-prey biomass balance equations (MB); and  
126 population-updating equations. Each component is described next.

127

### 128         **2.2.1. Individuals' Net Energy Functions in General**

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130         In GEEM, the sun is the source of all energy, and solar energy is converted to biomass by  
131 the two groups of primary producers (grass and shrubs). There is a fixed amount of land available  
132 where plants compete for light, acquire essential macronutrients (such as nitrogen), grow, and  
133 reproduce. The animals in the food web consume plants and other animals. Thus, solar energy  
134 enters the system through the plants and indirectly to the animals through herbivore foraging and  
135 predator-prey relationships. All solar energy entering the ecosystem is accounted for as energy  
136 leaving the system through respiration or as energy stored in the plants and animals (Tschirhart,  
137 2000). Predation risk is incorporated in the prey net-energy objective functions because it has been  
138 shown to be important in sage-brush ecosystems (Gude et al., 2006).

139         Each species  $i$ ,  $i = 1, \dots, 8$ , is comprised of  $n_i$  identical individuals that act as if they  
140 maximize the accumulation of net energy ( $R_i$ ) in every time period ( $t$ ). Plants choose their biomass  
141 accumulation via photosynthesis; animals choose their biomass consumption via grazing or  
142 predation. A general form for the net energy (measured in kcal) that an individual of species  $i$

143 accumulates is

$$144 \quad R_i(E, \mathbb{E}, X) = y_i(E, X) - r_i(X) - d_i(\mathbb{E}, X) - \beta_i \quad (1)$$

145 where  $E$  (kcal/kg) is either the set of energy expenditure prices for an animal preying on another  
146 animal or plant, or the energy expenditure price for a plant “preying” on the sun;  $\mathbb{E}$  (kcal/kg) is the  
147 set of the energy expenditure prices paid by the predators of species  $i$ ; and  $X$  (kg) is the set of  
148 biomass consumptions by an animal, or biomass growth of a plant. The functions in (1) represent  
149 inflows or outflows of energy:  $y_i(\dots)$  is the energy gain from predation or photosynthesis;  $r_i(\dots)$  is  
150 the energy loss from variable respiration;  $d_i(\dots)$  is the energy loss from predation and predation  
151 risk; and finally  $\beta_i$  is the basal metabolic rate which is the fixed cost of energy.

152 Each animal and plant maximizes net energy by balancing the gains and losses of biomass  
153 consumption. Animal gains come from energy embodied in the animal or plant biomass consumed,  
154 and the losses come from paying the energy prices, from predation avoidance, and from respiration  
155 that includes territory defense, locomotion, feces, and reproduction. Plant gains come from growing  
156 photosynthetic biomass and their losses come from respiration, animal foraging, and the energy lost  
157 by growing photosynthetic biomass.

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### 159 **2.2.2 Specific Individuals' Net Energy Function, FOC and Mass Balance**

160

161 By way of example, the net energy functions for an individual jackrabbit ( $i = Jr$ ) and an  
162 individual grass species ( $i = Gr$ ) are presented in (2) and (3), respectively. The two-letter indices in  
163 (2) - (4) are from Figure 1.

$$164 \quad R_{Jr}(E, \mathbb{E}, X) = (e_{Gr} - e_{Jr,Gr})x_{Jr,Gr} + (e_{Sh} - e_{Jr,Sh})x_{Jr,Sh} - \left( x_{Jr,Gr} + x_{Jr,Sh} + 0.5(x_{Jr,Gr}^2 + x_{Jr,Sh}^2 + \right. \\ 165 \quad \left. x_{Jr,Gr}x_{Jr,Sh}) \right) r_{Jr} - \beta_{Jr} \quad (2)$$

$$166 \quad R_{Gr}(E, \mathbb{E}, X) = (I_{Su} - SEL_{Gr}(L))\xi x_{Gr}S_{Gr} - r_{Gr}x_{Gr}^2 - \left( (1 + p_{Gr}(e_{El,Gr})) g_{El,Gr} + \right.$$

167 
$$\left(1 + p_{Gr}(e_{Jr,Gr})\right) g_{Jr,Gr} + \left(1 + p_{Gr}(e_{Ca,Gr})\right) g_{Ca,Gr} e_{Gr} x_{Gr}^{0.5} - \beta_{Gr} \quad (3)$$

168 where 
$$SEL_{Gr}(L) = (1 - \exp(-k_{Gr}L))I_{Su} \quad (4)$$

169 and 
$$L = \frac{1}{A}(n_{Sh}x_{Sh}S_{Sh} + n_{Gr}x_{Gr}S_{Gr}). \quad (5)$$

170 In (2), the first and second terms are the jackrabbit's incoming energy from consuming grass  
 171 and shrub, respectively. The total energy gained from grass is equal to the energy contained in each  
 172 kg of grass,  $e_{Gr}$ , times the kg of grass consumed  $x_{Jr,Gr}$ . The energy loss from foraging on grass is  
 173 the energy expenditure price times the kg of grass consumed:  $e_{Jr,Gr}x_{Jr,Gr}$ . Thus the first term is the  
 174 jackrabbit's net energy income from consuming grass. The second term is similar for the jackrabbit  
 175 consuming shrub.

176 Following Gurney and Nisbet (1998), jackrabbit (or other animal species) respiration is  
 177 divided into two parts: a variable part in the third term that depends on biomass consumption, and a  
 178 fixed part in the last term that is resting metabolic rate.<sup>2</sup> The form of the variable respiration  
 179 function implies that greater consumption yields greater respiration loss which follows because  
 180 animals that forage or hunt more use more energy in territory defense, locomotion, feces, and  
 181 reproduction. The two variable respiration terms have a quadratic form which allows for  
 182 specializing in one prey, or continuously substituting between prey which is more likely (Baalen et  
 183 al., 2001).

184 The net energy for a grass individual in (3) is similar to the jackrabbit net energy in (2). The  
 185 second term and last term are, respectively, a quadratic form for variable respiration and a constant  
 186 term for basal metabolism. The third represents the grass energy losses to its three foragers: elk,  
 187 jackrabbit, and cattle. However, the incoming energy given by the first term in (3) differs from the  
 188 jackrabbit, because plants derive their energy directly from the sun. In the first term,  $I_{Su}$  is the is the

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<sup>2</sup> Temperature and animal age are omitted from the metabolic rate but will be addressed in future research.

189 annual intensity of the sun's energy per square meter<sup>3</sup>;  $\xi$  is a parameter that measures the  
 190 percentage of energy that is effectively converted to glucose;  $x_{Gr}$  is the biomass (kg) that the  
 191 individual grows; and  $s_{Gr}$  is the ground area (m<sup>2</sup>) that grass photosynthetic biomass shades per kg.  
 192 The term  $SEL_{Gr}(L)$  in the first term of (3) is the shading energy loss that is comparable to the  
 193 energy prices paid by animals to capture prey, although here it is the energy price paid by the plant  
 194 for growing more biomass.

195 The third term in (3) is the energy that an individual grass loses to predation by elk,  
 196 jackrabbits, and cattle. This loss consists of the energy in the grass biomass lost to grazers, plus the  
 197 energy lost in avoiding predation. The former loss is interpreted as an average loss over all grass  
 198 individuals. The term  $e_{Gr}x_{Gr}^{0.5}g_{Jr,Gr}$  is the energy content of a kg of grass biomass,  $e_{Gr}$ , multiplied  
 199 by the average biomass lost to predation,  $x_{Gr}^{0.5}g_{Jr,Gr}$ . The  $g_{Jr,Gr}$  is a parameter that measures the rate  
 200 at which an individual grass supplies biomass to a jackrabbit, and the functional form of the  
 201 biomass loss is consistent with satisfying the second-order conditions for maximizing (2)  
 202 (Tschirhart, 2000). The parenthetical expression in the third term of (2) represents the energy lost in  
 203 avoiding predation, such as defense mechanisms or escaping. For example, some plants produce  
 204 noxious odors or repellent tastes to discourage predators. The more effort a predator must employ in  
 205 the hunt, the more energy the prey must use avoiding being captured. The function form for this  
 206 energy loss is assumed to be linear in the energy price paid by the predator,  $p_{Gr}(e_{Jr,Gr}) = p_{Gr}e_{Jr,Gr}$ ,  
 207 where  $p_{Gr}$  is a parameter that measures predation risk (Lima, 1998).

208 The energy gain of plants increases with the surface of their photosynthetic biomass, but

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<sup>3</sup> According to the Water Resources Data (2008), the solar insolation annual average for Wyoming is in between 5.1 and 5.5 kWh/m<sup>2</sup>/day, or 1,664,486 kcal/m<sup>2</sup>/year. Starting with the solar spectrum falling on a leaf, 47% is lost due to photons outside the active region (chlorophyll utilizes photons between 400 and 700 nm), 30% is lost due to incomplete absorption or absorption by components other than chloroplasts, and 24% is lost due to conversion of excitation energy at 700 nm to chemical energy of d-glucose (16, p. 4). Therefore, the sun intensity is  $1,664,486 * (1 - 0.3) * (1 - 0.47) * (1 - 0.24) = 469,318$  kcal/m<sup>2</sup>/year.

209 decreases with the shade created by their own leaves and the leaves of other plants. Therefore, the  
 210 space occupied by all the leaves imposes a cost on each individual plant; this explains why the  
 211 population and biomass accumulation of one plant species can affect other plant species. The SEL is  
 212 given in (4) and it is a function of the leaf area index,  $L$ , given in (5). The surface area occupied by  
 213 the leaves of an individual grass is  $x_{Gr}S_{Gr}$ ; the leaf area index sums these individual areas over all  
 214 shrub and grass individuals in (5) by multiplying the individuals' areas by the shrub and grass  
 215 populations, and dividing the result by  $A$ , the area of ARNG. The leaf area index is a measure of the  
 216 density of all plants: the higher (lower) the proportion of land used by plants, the higher (lower) the  
 217 SEL energy price paid by the plants for accumulating biomass.

218 The energy available for absorption per  $m^2$  of photosynthetic biomass will depend on the  
 219 orientation of the biomass; therefore, the leaf area index is multiplied by a species-specific  
 220 extinction coefficient,  $k_i$ , to account for the inclination of biomass surface area. Finally, the sun's  
 221 intensity minus the loss of energy to shading is multiplied by  $\xi = 32\%$  to account for the efficient  
 222 conversion of ATP and NADPH to d-glucose (Hall and Rao, 1999, p. 4).

223 Each individual acts as if it maximizes the net energy accumulated over a defined time  
 224 period which reflects the idea that the evolution of species must lead to an efficient use of energy  
 225 (Pennycuik, 1979; Yun et al., 2006). Optimization is a useful way of modeling efficient energy  
 226 use. The first-order conditions (FOCs) for optimization require setting to zero the derivatives of  
 227 each species' individual's net energy function with respect to the individuals choice variables. For  
 228 the jackrabbit presented above, the choice variables are the biomass consumptions,  
 229  $x_{Jr,Gr}$  and  $x_{Jr,Sh}$ , and for the grass the choice variable is the biomass growth,  $x_{Gr}$ . For example, the  
 230 FOC for jackrabbit consumption of grass is given by:

$$231 \quad \frac{\partial R_{Jr}(E, E, X)}{\partial x_{Jr,Gr}} = e_{Gr} - e_{Jr,Gr} - (1 + x_{Jr,Gr} + 0.5x_{Jr,Sh})r_{Jr} = 0 \quad (6)$$

232 Equation (6) indicates that at the optimum, the marginal benefit of consuming a kg of grass  
233 must equal its marginal cost. The first term is the jackrabbits's energy income from consuming a kg  
234 of grass. It is equal to two marginal losses from consuming the kg: paying the energy price (second  
235 term) and the marginal respiration loss (third term). If jackrabbit had any predator, then the  
236 marginal loss from being preyed on (which includes predation risk) should also be considered.

237 The FOCs provide the biomasses consumed by individual animals, and summing over all  
238 individuals in a species provides the species' biomasses consumed. To ensure mass balance in the  
239 model, it must be the case that the biomass consumed by one species must equal the biomass given  
240 up by the species consumed. Therefore, a mass balance equation is required for each demand/supply  
241 relationship between a predator and prey or grazer and plant. Equation (7) illustrates this category  
242 of equations for jackrabbit consumption of grass.

$$243 \quad n_{Jr}x_{Jr,Sh} = n_{Sh}x_{Sh}^{0.5}g_{Jr,Sh} \quad (7)$$

244 In the simulations, the FOCs and the mass-balance equations are solved for the biomass  
245 consumptions and the energy expenditures or prices. There are 9 FOCs (2 for plants and 7 for  
246 herbivores which includes cattle discussed below) and 7 mass balance equations (3 for grass-eaters  
247 and 4 for shrub-eaters). Essentially, there is one equation for every solid arrow in Figure 1, except  
248 for the arrows that connect plants and the sun<sup>4</sup>. The calculated biomasses and energy prices  
249 constitute a general equilibrium which is defined as a state of the ecosystem when all individuals  
250 are maximizing their net energy and mass balance holds over all species interactions. A general  
251 equilibrium holds in each period, but this does not imply a steady state in which populations are  
252 unchanging over time.

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<sup>4</sup> We assume that plants behave as if they are taking account of how their choice of biomass impacts overall shading (self-shading equilibrium). See Finnoff and Tschirhart (2009) for more details.

### 254            **2.2.3 Population Updating**

255            After a general equilibrium is calculated in each period, the resulting biomass and price  
256 values are used to update populations. Species' updates are based on annual energy accumulations  
257 of the average individuals, and on predation and death rates. Increasing (decreasing) populations  
258 correspond to positive (negative) individual net energy. If all populations are unchanging over time,  
259 then a steady state is said to be obtained.<sup>5</sup>

260            In steady state, the net energy for all the species is equal to zero except for cattle as  
261 explained below. Steady state implies that the average individual has accumulated exactly the  
262 necessary amount of energy to locate its prey, realize the activities related to respiration, avoid  
263 being hunted, expend its metabolic rate, and reproduce such that the deaths of old age (natural  
264 death) and predation are exactly offset by births. After a perturbation, the general equilibrium  
265 biomass and energy price values change which drive new population changes. If not in steady state,  
266 there are forces that tend to move the system to a new steady-state. For example, suppose that  
267 following a perturbation that individuals in a species have high optimum  $R_i$ . Then they will have  
268 high birth rates and the species' population will increase in subsequent periods. But high birth rates  
269 for a species will create more intraspecific competition and higher energy prices, thereby,  
270 decreasing individual's optimum  $R_i$ , and decreasing the population. Thus the impact of the initial  
271 perturbation is dampened by countervailing adjustments in the energy prices, and eventually  
272 individuals will move toward zero  $R_i$  and a new steady-state. The speed at which a new steady state  
273 is attained largely depends on the magnitude of the perturbation and on the responsiveness of plants.

274            Positive or zero prices follow from applying Kuhn-Tucker analysis to the general  
275 equilibrium optimization problem (see Tschirhart, 2012 for more detail). Formally we have the

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<sup>5</sup> The time step for GEEM is one year. This matches the reproductive cycle of the vertebrates, but we acknowledge that it is likely coarser than the processes for biomass accumulation of plants and leaf-area index growth.

276 following definitions of competition that will be applicable below in the Results:

277 Defn. 1: If the solution to the general equilibrium yields  $n_{Jr}x_{Jr,Gr} < n_{Gr}x_{Gr}^{0.5}g_{Jr,Gr}$  then  
278  $e_{Jr,Gr} = 0$  and there is said to be no competition among jackrabbit for grass.

279 Defn. 2: If  $e_{Jr,Gr} > 0$  then  $n_{Jr}x_{Jr,Gr} = n_{Gr}x_{Gr}^{0.5}g_{Jr,Gr}$  and there is said to be competition  
280 among jackrabbit for grass that is increasing in  $e_{Jr,Gr}$ .

281 The predation rate per capita for species  $i$  in the absence of satiation is:

$$282 \quad \text{PRD}_i(\mathbb{E}) = \frac{1}{w_i} \sum_{k \in K} \frac{n_k g_{k,i} x_{k,i}^{0.5}}{n_i} \quad (8)$$

283 where  $\mathbb{E} = \{e_{k,i} | k \in K\}$ ,  $w_i$  is the average individual's weight, and  $K$  is the set of all predators of  
284 species  $i$ . With satiation, the willingness to supply biomass ( $g_{k,i}x_{k,i}^{0.5}$ ) becomes the biomass  
285 demanded by the satiated predator, and it will be less than what the prey is actually willing to  
286 supply based on its own optimization problem. In that case, the term in the summation in (8) for  
287 satiated prey  $k$  is  $\frac{n_k x_{k,i}}{n_i}$ .

288 The natural death rate per capita is the percentage of the species' population that was not  
289 preyed upon during the current period and has lived an average lifespan. The average lifespan of an  
290 individual from the species  $i$  is denoted by  $l_i$ . If we assume that each species is divided into  $l_i$   
291 identically-aged groups, the groups have the same number of individuals, and the preyed upon  
292 individuals are evenly distributed among the groups, then the death (mortality) rate per capita of  
293 species  $i$  is:

$$294 \quad \text{DTH}_i(\mathbb{E}) = \text{PRD}_i(\mathbb{E}) + \frac{(1 - \text{PRD}_i(\mathbb{E}))^{l_i}}{l_i}. \quad (9)$$

295 The birth rate per capita depends on the amount of energy allocated to reproduction. We  
296 assume that the energy used for reproduction is a fixed portion of the sum of respiration and any  
297 additional energy accumulated during the relevant period. If at the undisturbed steady-state the net

298 energy is equal to zero and the birth rate is equal to the death rate, then the birthrate per capita of  
 299 species  $i$  is:

$$300 \quad \text{BTH}_i(E, \mathbb{E}, X) = \text{DTH}_i(\mathbb{E}_i^{\text{SS}}) \frac{\bar{R}_i(E, \mathbb{E}, X) + r_i(X)}{r_i(X_i^{\text{SS}})}$$

$$301 \quad \bar{R}_i(E, \mathbb{E}, X) = y_i(E, X) - r_i(X) - \bar{d}_i(\mathbb{E}) - \beta_i \quad (10)$$

302 where  $\bar{d}_i(\mathbb{E} = \{e_{k,i} | k \in K\}) = e_i \sum_{k \in K} \frac{1+t_i(e_{k,i})}{n_i} n_k x_{k,i}$ , since the relevant net energy accounts for  
 303 actual supply of biomass and not the willingness to supply it; also, the SS superscript indicates the  
 304 biomass accumulation, biomass consumptions, or energy expenditure prices are annual and  
 305 unchanging. Finally, the growth rate per capita (GTH) of species  $i$  is the birth rate minus the death  
 306 rate, or

$$307 \quad \text{GTH}_i(E, \mathbb{E}, X) = \text{DTH}_i(\mathbb{E}_i^{\text{SS}}) \frac{\bar{R}_i(E, \mathbb{E}, X) + r_i(X)}{r_i(X_i^{\text{SS}})} - \text{PRD}_i(\mathbb{E}_i) - \frac{(1 - \text{PRD}_i(\mathbb{E}_i))^{l_i}}{l_i}. \quad (11)$$

### 308 309 **2.3 Ecosystem Data and Calibration**

310 In the calibration we assume that the biomass accumulations, biomass consumptions, and  
 311 population densities depict an ARNG ecosystem in a scenario without NGD. This is a strong  
 312 assumption because the data obtained are contaminated by human disturbances. However, much of  
 313 our data comes from sources where the data were collected before major development in the  
 314 ARNG. Data were obtained for plant and animal populations ( $n_i$ ), plant biomasses ( $x_i$ ) and animal  
 315 biomass consumptions ( $x_{i,j}$ ), energy content per unit of biomass ( $e_j$ ), basal metabolisms ( $\beta_i$ ), plant  
 316 and animal weights ( $w_i$ ), lifespans ( $l_i$ ), predation risks ( $p_i$ ), solar intensity ( $I_{\text{Su}}$ ) and plant extinction  
 317 parameters ( $k_i$ ). These data and their sources are provided in table 1 of the Supplementary  
 318 Information section. Calibration is used to obtain parameter values that are not available in the  
 319 literature. These include: initial energy expenditure prices ( $SEL_i, e_{i,j}$ ), respiration function terms  
 320 ( $r_i$ ), and parameters in the willingness-to-supply functions ( $g_{k,i}$ ). In the calibration there are two net

321 energy ( $R_i$ ) equations for plant species and five net energy equations for animals, plus an equation  
 322 that defines the average annual weight gain ( $W$ ) once cattle is introduced to the ecosystem. These  
 323 equations are all set to zero to be consistent with a steady state.

324 There is very limited information in the literature for how much energy prey species use to  
 325 avoid predation. For plants, it was possible to define a value for  $p_i$  that would fit reasonable  
 326 assumptions (see the appendix of Finnoff and Tschirhart, 2008). In (12), non-green biomass  
 327 respiration of plant species is 39% of total incoming energy:

$$328 \quad 0.39 \exp \left( -k_i \frac{n_{Gr}^{SS} x_{Gr}^{SS} s_{Gr} + n_{Sh}^{SS} x_{Sh}^{SS} s_{Sh}}{109339} \right) \xi I_{Su} s_i x_i^{SS} = \beta_i \quad (12)$$

329 which follows from considering that the percent of carbohydrates produced in photosynthesis  
 330 consumed in non-green respiration for slow-growing grass species is 16% by roots and 25% by  
 331 shoots Lambers et al. (2006).<sup>6</sup> This adds conditions to the calibration and allows solutions for the  
 332 predation risk of plants.

## 333 334 **2.4 Plant Competition and Nitrogen**

335 Subject to caveats, the resource/ratio hypothesis states that the number of competing plant  
 336 species can be no greater than the number of limiting resources (Tilman, 1985; Miller et al., 2005).  
 337 GEEM is consistent with the resource/ratio hypothesis (Finnoff and Tschirhart, 2009); because there  
 338 are two plant species in the ARNG model, nitrogen is introduced as a second resource to allow  
 339 coexistence of the plant species. The availability of nitrogen is the primary factor limiting plant  
 340 growth in many ecosystems (Chapin et al., 1986; Tilman et al., 1996), and in a prairie system the  
 341 competition between grasses and shrubs is strongest for nitrogen (Kochy and Wilson, 2000). In the  
 342 model there is a restriction that limits how much nitrogen can be absorbed from divergent layers of

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<sup>6</sup> This yields  $\frac{16}{16+25} = 39\%$  for the non-green biomass.

343 soil according to the grass versus shrub root structures and biomass accumulations. This absorption  
344 of nitrogen then regulates plant growth and biomass accumulation. The details on how nitrogen  
345 enters the model and how the plants compete for it are in the Supplementary Information section.

## 346 347 **2.5 Ecosystem Services: Grazing and Hunting**

348 The seven native ARNG species use a portion of their energy to reproduce, and when prey  
349 or forage is abundant, these species expend less energy and reproduce at a greater rate. Cattle,  
350 however, are assumed to use their acquired energy to gain weight rather than reproduce. The net  
351 energy of cattle must be positive at the steady state because ranchers will introduce cattle only if  
352 they gain weight, that is, their net energy is positive. Therefore, to complete the calibration, some  
353 assumptions regarding the profitability of grazing cattle are needed.

354 Ranchers are assumed to employ a stocker operation where they acquire young adult steers  
355 or heifers and graze them for one season before they are sent to market. Since much of this grazing  
356 occurs on public land under grazing permits, the density of cattle on the rangeland ecosystem is, at  
357 least in part, under the control of the BLM. Following the literature, a stocking rate for steers or  
358 heifers of 0.22 (0.57, 0.90) per ha is considered low (heavy, very heavy) density (Hart and Ashby,  
359 1998; Derner and Hart, 2007; Jablonski et al., 2018). For the ARNG density, according to the EIS  
360 there are 31 relevant BLM grazing allotments in the ARNG and the surrounding area, which allows  
361 for a total of 39,695 animal unit months (AUMs). Assuming the number of AUMs inside the ARNG  
362 is proportional to its acreage yields 21,135 AUMs. Also assuming each animal is allowed to graze  
363 five months implies a total of 4,227 individual steers and heifers. Since there are 109,297 ha in the  
364 ARNG, the estimated grazing density is  $4,227/109,297 = 0.0387$  animals per hectare. This density is  
365 lower than what the literature considers low density, but many of those studies refer to more fertile  
366 land and dense grass.

367 Cattle consume only grass as shown in Figure 1, which puts them in direct competition with  
 368 the native grass-eaters. We assume that a new steady-state occurs after cattle are introduced to the  
 369 ecosystem, where individuals consume enough grass biomass to gain 180 kg of additional weight by  
 370 the end of the stocking season. If the initial weight is 247 kg and cattle consume about 1.2 kg per  
 371 day during an average stocking season of 150 days (i.e., about five months), the weight of each  
 372 individual at the end of the stocking season is 427 kg.

373 The consumed energy of an individual stocker can be converted to an average annual weight  
 374 gain ( $W$ ) in kg with the formula (National Research Council, 2000):

$$375 \quad W(R_{Ca}) = \frac{182.5}{0.956} \left( \frac{R_{Ca}}{182.5(1000)} \right)^{\frac{1}{1.097}} \left( \frac{1}{0.0635(0.891w_b)^{0.75}} \right) \quad (13)$$

376 where  $R_{Ca}$  is the net energy in kcal for each individual stocker over a grazing season and  $w_b$  is the  
 377 average weight when introduced into the ecosystem. The weight gain cannot be less than zero. In  
 378 the calibration of the model, we assume that ranchers introduce 4,227 individuals, and after the  
 379 ecosystem reaches a steady state, each individual consumes 1,326 kg of grass biomass.<sup>7</sup> By using  
 380 these values and solving for  $R_{Ca}$  in equation (13), every individual stocker is able to accumulate  
 381 620,801 kcal within a year to meet the goal weight. The following equation to calculate the profit  
 382 per period for cattle ranchers ( $\Pi_{Ca}$ ) has been proposed in previous research on cattle grazing  
 383 activities (Hussain and Tschirhart, 2013):

$$384 \quad \Pi_{Ca} = \left( (W(R_{Ca}) + w_b)p_f - w_b p_b \right) n_{Ca} \quad (14)$$

385 where  $n_{Ca}$  is the population of cattle introduced to the ecosystem;  $p_f$  is the price per kg for a  
 386 stocker at the end of the period; and  $p_b$  is the price per kg for a stocker at the beginning of the

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<sup>7</sup> Weights of stocked cattle vary. We use typical weights of 247 kg per stocked feeder calf and 427 kg market weight at the end of the stocking season based on Derner et al. (2008). According to Hironaka and Freeze (1992), one animal unit requires 11.8 kg of dry matter per day per 450 kg of body weight. This was adjusted for the different weights and summed over 150 days.

387 period. The total weight of an individual stocker at the end of the period is the sum of the initial  
 388 weight plus the weight gained, and therefore the total benefit of grazing cattle is the total weight  
 389 times the final price. The economic cost of cattle grazing is the weight of the individual stocker at  
 390 the beginning of the period multiplied by the input price. The total ARNG ranching profit is the  
 391 number of cattle introduced times the profit per individual. Neither the  $W$  nor the profits can be  
 392 negative since equation (13) does not allow negative net energy values. Introducing cattle requires  
 393 including another  $R$  equation, its corresponding FOCs, and a MB equation.

394         Once GEEM is calibrated to be consistent with the nitrogen restriction and the natural  
 395 rangeland ecosystem, first cattle are introduced, and, once a new steady-state occurs, then hunting is  
 396 introduced. Hunting is modeled as a percentage reduction of the elk, pronghorn, and mule deer  
 397 populations at the end of each period. The percentage, or hunting rate, is fixed but the number of  
 398 harvested animals varies over time. To calibrate GEEM for recent hunting rates, we collected 2014  
 399 data from published Wyoming Game and Fish Department (WGFD) harvest reports. The hunting  
 400 areas (or units) intersect with the ARNG region but none falls entirely inside. We calculated the  
 401 percentage of each unit that falls inside the ARNG region, and then assumed that the same  
 402 percentage of elk, pronghorn, and mule deer from the total animals hunted were harvested inside the  
 403 ARNG region. The population of the hunted species (SH) during period  $t + 1$  is

$$404 \quad n_i^{t+1} = (1 + GTH_i(E_i, \mathbb{E}_i, X_i))n_i^t - h_i^{t+1} \quad (15)$$

405 where  $n_i^t$  is the population of the hunted species  $i$  at the end of period  $t$  and  $h_i^{t+1}$  is the number of  
 406 individuals hunted from the species  $i$  during period  $t + 1$ .

407         The estimation of hunting net benefits ( $\Pi_{Hu}$ ) is based on previous research that uses GEEM  
 408 and calculates the value of the ecosystem services (Hussain and Tschirhart, 2013). We adapted the  
 409 net benefits by making the cost of hunting a function of the total number of hunters:

$$410 \quad \Pi_{Hu} = \sum_{i \in SH} ((m_i + V(n_i))h_i + (\tau(h_i) - h_i)V(n_i)) - C(\sum_{i \in SH} \tau(h_i)) \quad (16)$$

411 where  $h_i$  is the number of individuals animals harvested from species  $i$  and  $m_i$  is the meat value of  
 412 an animal. The function  $\tau(\dots)$  is the total number of hunters (or hunter congestion) that is increasing  
 413 in  $h_i$ , that is  $\tau'(h) > 0$ ; and  $C(\tau) = 64\tau^{0.9}$  is the cost function for hunting trips. The number of  
 414 hunters,  $\tau(h_i)$ , and the harvest,  $h_i$ , are not equal because not all hunters are successful (i.e., to hunt  
 415  $h_i$  animals, more than  $h_i$  hunting licenses must be issued). Also, the function  $V(n) = \frac{4200n^{0.8}}{3.5n+1.6}$   
 416 represents the value of the trip itself regardless of successful hunting, where the hunters experience a  
 417 benefit from observing wildlife during the trip. As a result, the value of the trip increases whenever  
 418 the population of wildlife increases:  $V'(n) > 0$ , because the trip includes various subjective (or  
 419 non-pecuniary) benefits enjoyed on a hunting trip. The formulation in (16) shows that meat value is  
 420 enjoyed only for a successful hunter, but the trip value is enjoyed by all hunters. We used the same  
 421 functions described in Hussain and Tschirhart (2013) except for the function  $\tau(h + i)$ . We use

$$422 \quad \tau(h_i) = \frac{h_i}{SR_i} \quad (17)$$

423 where  $SR_i$  is the success rate for hunting the hunted species  $i$ .<sup>8</sup> The average success rate and the  
 424 hunting rates used for elk, pronghorn, and mule deer during the simulations are presented in the  
 425 supplemental information section.

426

## 427 **2.6 Energy Development and Disturbed Areas**

428 Previous research has found that various species avoid natural-gas wells, but the magnitude  
 429 of the impact depends on the intensity of the development, the affected species, and the season  
 430 (Kauffman et al., 2018). A study of the Powder River Basin in Wyoming and Montana shows that  
 431 coalbed methane/natural gas development has a negative impact on sage-grouse leks, with the

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<sup>8</sup> For example, if the success rate of elk is 50%, then 100 hunting licenses must be issued in order to have 50  
 successfully hunted elk ( $\tau(50) = \frac{50}{0.5} = 100$ ).

432 disturbed region ranging somewhere between 0.8 km and 3.2 km from the wells (Walker et al.,  
433 2007). Doherty et al. (2008) estimate that sage grouse were 1.3 times less likely to occupy  
434 sagebrush habitat in a 4 km<sup>2</sup> area around coalbed methane/natural gas wells (equivalent to a circle  
435 with radius of 1.13 km). Similarly, studies suggest that elk and mule deer avoid oil and gas  
436 development areas (Hebblewhite, 2011). In particular, elk avoided areas within 2 km of major roads  
437 and active gas/oil wells during the summer and 1 km during winter (Powell, 2003), and mule deer  
438 have a higher probability to avoid areas up to 3.7 km from gas development (Sawyer et al., 2006).  
439 However, Van Dyke et al. (2012) show that elk in particular are capable of modifying their behavior  
440 in response to habitat disturbances if they can find alternative routes where forage is sufficiently  
441 abundant.

442 To account for the impact of NGD, we assume that elk, mule deer, and sage grouse  
443 experience stress whenever they forage inside the areas surrounding the natural-gas well which are  
444 labelled “disturbed areas” (DAs). Stress is included in the model by assuming that the animals lose  
445 energy depending on how much time they spend foraging in the DAs; if biomass consumption  
446 occurs in the the undisturbed area (UA), no additional losses are experienced by the animal.<sup>9</sup> There  
447 are three DAs in total, the first DA is located within a radius of 500 m around all well pads;  
448 meanwhile, the second DA is located between 500 and 1,000 m from the closest well pad, and the  
449 third one is located between 1,000 m and 1,500 m; the area outside the DAs is labelled UA. Based  
450 on the evidence above, we assume that elk are less sensitive to NGD, therefore, they experience the  
451 lowest levels of stress when exposed to NGD in each DA; meanwhile, the mule deer are the most

---

<sup>9</sup> For example, the energy that elk (El) gain from grazing upon grass at the UA are  $(e_{Gr} - e_{El,Gr,UA})x_{El,Gr,UA}$ , while the losses at the DA3 are  $-e_{Gr}x_{El,Gr,DA3}\delta_{DA3}$  where  $\delta_{DA3}$  is a parameter that measures sensitivity to NGD in DA3. If  $\delta_{DA3} = 1$ , elk would not gain any energy by grazing in DA3 because the stress is at its highest value; conversely, if  $\delta_{DA3} = 0$ , elk would not experience any stress by grazing in DA3.

452 sensitive to NGD; finally, sage grouse are not as affected as mule deer but more affected than elk.<sup>10</sup>  
453 All other species in the rangeland ecosystem forage in the DAs and UA without experiencing any  
454 stress. A simple schematic of habitat loss and NGD stress is shown in Figure 2.

455 Figure 3 shows the location of the active natural-gas wells in 2010 and the total DA in the  
456 ARNG region from 1980 to 2010 assuming the three different radii around each well. Figure 4  
457 shows the number of wells that were active in each year from 1980 to 2010. Although the number  
458 of wells has generally been growing, it started increasing sharply in 1998. For tractability, we  
459 assume that all gas wells new since 1999 are assumed to be introduced simultaneously. Absent this  
460 assumption, all the DAs in the model would need to be indexed by their age. Given the DAs, the  
461 total affected area is equal to 20,889 ha or 19% of the ARNG area.<sup>11</sup> Interestingly, the maximum  
462 allowable DA in the EIS is significantly smaller (BLM, 2007), but the EIS only considered actual  
463 cleared habitat and not the avoided area around gas wells. The EIS plan calls for active reclamation  
464 that would stabilize disturbed soils and vegetation communities, while allowing for no more than  
465 3,075 ha of total DA (3% of the total ARNG area) at any time.

466

### 467 **3 Results**

468 Given the lack of complete ecological and economic data for the ARNG region, the model is  
469 calibrated using ecological parameters, economic parameters, and functional forms that are  
470 sometimes imprecise. Therefore, we quantify the inherent uncertainty in the model's predictions by  
471 undertaking a thorough sensitivity analysis whereby the parameter values are varied up and down

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<sup>10</sup> In our baseline scenario, we assumed that elk experience some stress (0.2) in the DA3, experience stress at a sensitivity of 0.5 in the DA2, and 0.8 in the DA1; sage grouse experience stress at the level of 0.25, 0.55, and 0.85 in DAs 3, 2, and 1, respectively; finally, mule deer experience stress at the level of 0.7, 0.8, and 0.9 in DAs 3, 2, and 1, respectively.

<sup>11</sup> The total unaffected area is 88,408 ha. The total affected area is comprised of 10,193 ha for the DA1 that produces the highest stress on the affected species; 5,187 ha for the DA2 that produces a moderate stress; and 5,509 ha for the DA3 that produces the lowest stress.

472 by a fixed percentage. The results of the sensitivity analysis are shown in the Supplementary  
473 Information section and will be discussed in more detail below.

474 Figure 5 shows the simulated time paths for plant biomasses and animal populations for  
475 various combinations of disturbances. The top panel of Figure 5 shows the time paths for four  
476 scenarios before NGD. In the first scenario, the ecosystem starts at the natural undisturbed steady  
477 state; then cattle grazing is introduced for scenarios 2 and 4. Once the system settles down to a new  
478 post-ranching steady state, hunting is introduced for scenarios 3 and 4. In the bottom panel of  
479 Figure 5, the simulations continue and NGD is introduced starting at the post-disturbance steady  
480 states from the four scenarios in the top panel of Figure 5. We discuss the simulations results below.

481

### 482 **3.1 Responses to Hunting in GEEM**

483 As expected, the introduction of elk, pronghorn and mule deer hunting immediately  
484 increases the amount of forage available for surviving individual herbivores. Hunting also indirectly  
485 impacts plants; consider grass first. With fewer elk after hunting, the population of grass increases  
486 (for both, “cattle grazing” and “cattle grazing + hunting” scenarios). However, nitrogen limits the  
487 total biomass of grass such that a new steady-state is attained with a larger population of smaller  
488 plants as shown in the Supplementary Information (Bai et al., 2012). Meanwhile, even though there  
489 are fewer pronghorn and mule deer, the population of shrubs decreases. The energy price shrubs  
490 expend to grow biomass increases because of interspecies competition fueled by the higher total  
491 biomass of grass. This in turn leads to a smaller population of smaller shrubs. Even though both  
492 plant species experience less pressure from herbivores, grass partially displaces shrubs. This follows  
493 because after hunting, total elk consumption (individual consumption times population) of grass  
494 biomass as a percent of total grass biomass decreases, whereas total deer plus pronghorn  
495 consumption of shrub biomass as a percent of total shrub biomass increases. After the initial

496 responses from hunting, grass and shrub populations converge slowly to a new post-hunting steady  
497 state.

498         The impact on non-hunted species depends on their plant consumption and whether they  
499 have competitive relationships with other animals. For example, removing elk benefits cattle by  
500 lowering inter-specific competition because removal lowers the energy price cattle pay for grass.  
501 The effect on sage grouse is particularly interesting since their population decreases even though  
502 this species is not hunted. This negative impact on sage grouse occurs because elk hunting releases  
503 more foraging pressure on grass than pronghorn and mule deer hunting on shrubs, which is the  
504 primary food source of sage grouse. This result would not hold if only elk were hunted. Interactions  
505 between the forage consumption patterns of ungulates and their interactions with other key species,  
506 such as cattle, have been studied by authors such as Hobbs et al. (1996) who found that higher elk  
507 density lowers forage intake by cattle through competitive effects.

508         The combination of cattle grazing and hunting results in completely different population  
509 dynamics. If only hunting is considered but no cattle grazing, the sage-grouse population is slightly  
510 lower than the undisturbed scenario. If only cattle grazing is considered, the sage-grouse population  
511 is significantly higher than at the undisturbed scenario. When both economic activities are  
512 considered, the sage-grouse population is higher than in the undisturbed case but lower than when  
513 only cattle grazing is modeled.

### 514 515 **3.2 Predicted Ecological Impacts of NGD**

516         Plants are affected by NGD because the mix of herbivores that consume them differ between  
517 the UA and DAs; in particular, elk, mule deer, and sage grouse are less willing to forage in the DAs.  
518 The populations of the directly affected species will initially decline because they gather less energy  
519 in the relatively more congested UA, but this impact can be (partially) reversed if the forage

520 availability redistribution favors them. Other herbivores will choose to forage relatively more  
521 heavily inside the DA after NGD due to less inter-specific competition. This result can be seen in  
522 the general equilibrium calculations pre- and post-NGD. As discussed in Section 2 above, to attain  
523 an ecosystem general equilibrium in each period, an individual herbivore's marginal energy gains  
524 inside the DA and the UA must be equal. This follows because if a herbivore enjoyed greater  
525 energy gain in the DA, for example, it would switch to more DA grazing which would increase the  
526 DA's energy price and lower the UA's energy price. This behavior would continue until the energy  
527 prices stabilize and the incentive to switch vanishes. In effect, the effort that it takes for animals to  
528 find prey must be equal inside and outside the DAs and UA, which is consistent with the marginal-  
529 value theorem (Charnov, 1976; Stephens and Krebs, 1986).

530         The negative impact of NGD on the species in the short-run can reverse in the long-run. In  
531 the short run, the species that experience no stress when foraging close to the well pads are better  
532 off. For example, when NGD is introduced to the ecosystem, sage grouse and mule deer  
533 significantly reduce their foraging in the DAs, allowing pronghorn and jackrabbits (which do not  
534 experience stress when foraging in the DAs) to take advantage of the higher abundance of forage  
535 near the disturbance. This leads to a population increase in pronghorn and jackrabbits and a decline  
536 in sage grouse and mule deer. However, this dynamic is a short-term phenomenon and only part of  
537 the story. In the long run, the two plant species will compete for space, sunlight and nitrogen with  
538 the plant species receiving less pressure from foragers outcompeting the other plant species over  
539 time (Pfeiffer et al., 2019). For our calibration, shrubs in the DA experience relatively less forage  
540 pressure than grass, and as a result, the population of grass in the DAs eventually declines and the  
541 population of shrubs increases until a new steady-state is reached.

542         The long-run population dynamics of introducing NGD can offset some of the damage  
543 caused in the short-run. For example, sage grouse choose to forage much less in the DAs, which in

544 turn leads to a decrease in their population. Depending on which economic activities are considered  
545 previous to the introduction of NGD, the population of sage grouse may partially recover before  
546 reaching a new steady-state. For our baseline calibration, sage grouse populations fluctuate between  
547 a loss of 1.4% (NGD scenario) and 7.7% (Cattle Grazing + NGD scenario) by comparing pre- and  
548 post-disturbance steady states. Nevertheless, the population of sage grouse can drop as low as  
549 13.1% in the short run (Cattle Grazing + NGD scenario). The impact of NGD on elk populations  
550 fluctuates between a decrease of 13.2% (Hunting + NGD scenario) and a decrease of 18.5% (Cattle  
551 grazing + NGD scenario). Positive effects on the populations of directly impacted species are less  
552 likely to occur when the sensitivities to NGD are higher; these scenarios are explored in the  
553 appendix.

554

### 555 **3.3 Impacts on Ecosystem Services**

556 Here we calculate the impact of NGD on the value of ecosystem services (i.e., cattle  
557 ranching, hunting, and the existence value of sage grouse) in the ARNG region. Although sage  
558 grouse are only one of many species in the ARNG ecosystem, they are a high-profile species that  
559 have been repeatedly considered for listing under the U.S. Endangered Species Act (FWS, 2015a).  
560 The species also receives significant media attention such as the recently publicized plans of the  
561 Trump Administration to ease oil and natural-gas drilling restrictions given in the Greater Sage-  
562 Grouse Resource Management Plan.<sup>12</sup>

563 The total discounted sum of the values of the ecosystem services (TDVES) is defined as

564 
$$TDVES = \lim_{T \rightarrow \infty} \sum_{t=t_{NGD}}^T \frac{\pi_{Ca}^t + \pi_{Hu}^t + \pi_{Sg}^t}{(1+r)^{t-t_{NGD}}} \quad (18)$$

565 where  $t_{NGD}$  is the time period when NGD is introduced,  $\pi_{Ca}^t$  is the profits of cattle ranching in

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<sup>12</sup> [https://www.doi.gov/sites/doi.gov/files/uploads/so\\_3353.pdf](https://www.doi.gov/sites/doi.gov/files/uploads/so_3353.pdf)

566 period  $t$ ,  $\pi_{Hu}^t$  are the net benefits of hunting,  $\pi_{Sg}^t$  is the existence value of sage grouse, and  $r$  is the  
567 discount rate (set at 3% in the simulations). In Section 2 of the Supplementary Information, we  
568 describe in detail the calculations regarding the existence value of sage grouse.

569         The animals that are willing to graze close to the well pads are better off in the short run,  
570 which has an effect on the value of the ecosystem services associated to them. Figure 6 shows the  
571 annual value of the ecosystem services over the same time period and combination of economic  
572 activities as used in Figure 5. Cattle accumulate more net energy by foraging in the less crowded  
573 DAs because elk avoid the well pads, and the profits of cattle grazing increase in the short run.  
574 Meanwhile, the net benefits of overall hunting decrease because the reduced net benefits of hunting  
575 mule deer and elk (species that avoid well pads) more than compensate the increased net benefits of  
576 pronghorn hunting (species that are willing to graze close to well pads).

577         The net benefits of hunting continue to decrease in the long run, the profits of cattle grazing  
578 fall in the long run, and the existence value of sage grouse recovers from the initial drop. The main  
579 message from Figure 6 is that while NGD leads to a decrease in TDVES, the size of the total loss  
580 and the stakeholder groups that experience losses vary significantly depending on which  
581 disturbances and economic activities are modeled.

582

#### 583 **4 Discussion**

584         Previous studies have tended to focus on how NGD affects a narrow set of species, such as  
585 caribou and elk, without analyzing the feedback paths from the rest of the species in the food web  
586 (Sorensen et al., 2008; Wasser et al., 2011; Dzialak et al., 2011). The advantage of using GEEM is  
587 that a multi-species food web can be used to capture the feedback effects and the ecosystem  
588 externalities that cattle ranching, hunting, and NGD impose on each other. This is important  
589 because policymakers, scientists and academics might draw the wrong conclusions about ecosystem

590 management if the models used only consider a small number of species or do not involve the  
591 complex feedback mechanisms. Policymakers could also draw incorrect conclusions or  
592 unintentionally misinform the public if they do not fully account for the larger disturbed area caused  
593 by NGD when publishing Environmental Impact Statements (BLM, 2007).

594         As an illustration, consider the impacts in Figure 6. The profits of cattle ranching are nearly  
595 seven times lower if only cattle grazing and NGD are assessed but hunting is not modeled (Grazing  
596 + NGD vs. Grazing + Hunting + NGD scenarios) because the positive ecosystem externalities that  
597 hunters impose on ranchers are not taken into account. Similarly, if only hunting is considered and  
598 the impact of cattle grazing is ignored, the GEEM model estimates lower net benefits of hunting  
599 because the positive externality that ranchers impose on hunters is ignored. Although it is hard to  
600 appreciate in Figure 6, the ecosystem externalities do not simply “stack up”; the negative impact of  
601 NGD may be exacerbated or dampened depending upon which other economic activities are  
602 modelled.

603         The pure negative impact of NGD (by contrasting the pre- and post-development SSs) on  
604 the profits of cattle ranching is \$0.1 million higher if hunting is ignored and only grazing activities  
605 are considered. Analogously, the negative impact of NGD on the net benefits of hunting is \$0.02  
606 lower million if cattle grazing is ignored and only hunting activities are considered. Although these  
607 impacts are relatively small for cattle grazing and hunting, the negative impact can be much larger  
608 depending upon the circumstances. In the case of the existence value of sage grouse, the negative  
609 impact of NGD is \$0.83 million when hunting and cattle grazing are considered but it can be as low  
610 as \$0.11 million if neither hunting nor cattle grazing are considered or as high as \$1.09 million if only  
611 cattle grazing is considered.

612         Another advantage of addressing the interactions of cattle grazing, hunting and NGD in  
613 GEEM is that it more accurately reflects the long-run population dynamics. When only NGD is

614 considered without the other disturbances, the sage grouse population is predicted to experience a  
615 fairly rapid partial recovery after the initial decline, which seems at odds with the empirical  
616 evidence.

617         We highlight two other findings of our research. First, although NGD provides substantial  
618 economic benefits to society, it generally harms biodiversity (Xiao et al., 2018). Although overall  
619 biodiversity falls after NGD, it has the potential to create winners and losers in terms of species'  
620 populations. On the one hand, species such as sage grouse, mule deer, and elk that avoid the area  
621 around the natural-gas wells will lose habitat and experience population declines. On the other  
622 hand, the populations of herbivores that are willing to graze in the DAs may increase due to reduced  
623 forage competition. The introduction of NGD also creates winners and losers in terms of ecosystem  
624 services, but similar to the population dynamics, the wins/losses can be amplified or reversed  
625 depending upon the disturbances modeled and the sensitivity of the species to NGD.

626         Second, there are important ecosystem externalities that hunting and cattle grazing, and the  
627 agencies that represent them, impose on each other. Given this context, it is necessary to promote  
628 coordination between these economic agents to reach a social optimum, particularly after the  
629 introduction of NGD. For example, a higher elk hunting rate will cause cattle to experience less  
630 competition for grass, gain more weight, and increases the overall value of ecosystem services. In  
631 terms of biodiversity, decreasing the density of cattle will cause grass to become more abundant,  
632 ameliorating the reduction in the elk population caused by NGD. This implies that the energy  
633 companies, WGFD officials, and BLM officials can coordinate to generate a management strategy  
634 that balances energy production, changes in ecosystem services, and potential losses in biodiversity.  
635 Crawford et al. (2004) show the linkage of habitat and population dynamics of sage grouse by  
636 considering factors such as the effects of fire-ecology, cattle grazing, and herbicide-based control of  
637 big sagebrush; they conclude that solving management issues associated with the decline of sage

638 grouse will require cooperation among wildlife biology, range science, and other professional  
639 abilities (see Section 4 of the Supplementary Information for a detailed analysis of the possible  
640 coordination failures and the opportunities to mitigate the loss of ecosystem services and  
641 biodiversity). Our research supports this conclusion.

642         We close by mentioning a few caveats to our work. First, there is substantial uncertainty in  
643 some of the calibrated parameters and modeling assumptions. We vary parameters related to: (1) the  
644 sensitivity to NGD of the affected species, (2) the availability and plant uptake of nitrogen in the  
645 soil layers, and (3) the existence value for sage grouse per household. In all cases, the impact of  
646 introducing NGD is negative and measured in terms of the total discounted value of ecosystem  
647 services (TDVES), the loss varies between -\$0.12 and \$81.67 million in the baseline scenario.<sup>13</sup> As  
648 a reference point, the negative impact estimated in our baseline scenario is \$58.40 million. See  
649 Section 3 of the Supplementary Information for further details.

650         Second, there are other factors besides nitrogen and light that restrict plant growth. For  
651 example, we included the role of precipitation in the model as a random variable, where plants that  
652 are exposed to less than ideal amounts of water experience stress. The results from modeling  
653 precipitation were not fundamentally different than the results presented here. Therefore, we  
654 decided to focus exclusively on nitrogen and sunlight restrictions in this paper and explore the role  
655 of precipitation in future research.

656         Third, plants and animals may be impacted by NGD for various reasons. For example,  
657 studies show that sage-grouse populations may decline if established leks are abandoned due to  
658 increased human or predator activity from the introduction of roads and power lines (Ellis 1984;  
659 Lyon and Anderson, 2003; Holloran, 2005; Kaiser, 2006; Doherty et al., 2008). Also, our research

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<sup>13</sup> The lower bound on the loss from NGD is negative and indicates a benefit of NGD in terms of TDVES. However, the number is relatively small, approximately \$120,000, and the vast majority of the range of estimates indicate a TDVES loss from NGD.

660 does not address the carnivore-herbivore interactions (such as coyotes, ferrets, and swift foxes) and  
661 some other herbivores (such as grasshoppers and prairie dogs) that could play an important role in  
662 the sagebrush ecosystem; we have observed that plants' reactions to disturbances tend to be more  
663 pronounced when fewer species are considered. Another limitation of the model is that it does not  
664 explicitly model space or the migration of species over the landscape. This is something we are  
665 currently working on adding to the GEEM framework. Finally, in future research we intend to  
666 further investigate other modelling assumptions such as those related to boundary issues, water as a  
667 limiting resource, and plant competition for sunlight.

668         Lastly, one of the main advantages of using a model such as GEEM is that it provides a  
669 unified framework for modeling the various interactions within a food web. The downside is that  
670 like many models, it oversimplifies animal and plant behaviors. Therefore the goal of our research  
671 is not to provide precise predictions of how human development impacts an ecosystem, but rather to  
672 inform government agencies and relevant stakeholder groups, at a high-level, how various  
673 economic activities and species interact within an ecosystem.

674 **References**

- 675 Abrams, P.A. 1999. The adaptive dynamics of consumer choice. *American Naturalist*, 153, 83-97.
- 676 Baalen, M.V., Krivan, V., van Rijn, P.C.J., and Sebelis, M.W. 2001. Alternative food, switching  
677 predators, and the persistence of predator-prey systems. *American Naturalist*. 157: 153-62.
- 678
- 679 Bai, Y., Wu, J., Clark, C.M., Pan, Q., Zhang, L., Chen, S., Wang, Q. and Han, X., 2012. Grazing  
680 alters ecosystem functioning and C: N: P stoichiometry of grasslands along a regional precipitation  
681 gradient. *Journal of Applied Ecology*, 49(6), 1204-1215.
- 682
- 683 Brady, W.A., Smith, W.K., Twidwell, D., Haggerty, J.H., Running, S.W., Naugle, D.E. and  
684 Fuhlendorf, S.D. 2015. Ecosystem services lost to oil and gas in North America. *Science*. 348(6233),  
685 401-02.
- 686
- 687 Chapin, F., Vitousek, P., and Van Cleve, K. 1986. The nature of nutrient limitation in plant  
688 communities. *The American Naturalist*, 127(1), 48-58.
- 689
- 690 Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*,  
691 9, 129-136.
- 692
- 693 Chermak, J. and Patrick, R.H. 1995. A well-based cost function and the economics of exhaustible  
694 resources: The case of natural gas. *Journal of Environmental Economics and Management*, 28(2),  
695 174-189.
- 696
- 697 Crawford, J. A., Olson, R. A., West, N. E., Mosley, J. C., Schroeder, M. A., Whitson, T. D., and  
698 Boyd, C. S. 2004. Ecology and management of sage grouse and sage-grouse habitat. *Journal of Range  
699 Management*, 57(1), 2–19.
- 700
- 701 Crocker, T. D., and Tschirhart, J. 1992. Ecosystems, externalities, and economies. *Environmental and  
702 Resource Economics*, 2(6), 551–567.
- 703
- 704 Davies, K. W., Bates, J. D., and Nafus, A. M. 2010. Vegetation characteristics of mountain and  
705 Wyoming big sagebrush plant communities in the Northern Great Basin. *Rangeland Ecology  
706 Management*, 63, 461–466.
- 707
- 707 Derner, J. and Hart, R. 2007. Grazing-induced modifications to peak standing crop in northern mixed-  
708 grass prairie. *Rangeland Ecology and Management*, 60(3):270–276.
- 709
- 710 Doherty, K. E., Naugle, D. E., Walker, B. L., and Graham, J. M. 2008. Greater sage-grouse winter  
711 habitat selection and NGD. *Journal of Wildlife Management*, 72, 2644–2654.
- 712
- 712 Dzialak, M. R., Webb, S. L., Harju, S. M., Winstead, J. B., Wondzell, J. J., Mudd, J. P., and Hayden-  
713 Wing, L. D. 2011. The spatial pattern of demographic performance as a component of sustainable  
714 landscape management and planning. *Landscape Ecology*, 26, 775–790.
- 715
- 716

- 717 Ellis, K. L. 1984. Behavior of lekking sage grouse in response to a perched golden eagle. 715 *Western*  
718 *Birds*, 15, 37–38.
- 719
- 720 Estes, J., Tinker, M., Williams, T., and Doak, D. 1998. Killer whale predation on sea otters linking  
721 oceanic and nearshore ecosystems. *Science*, 282(5388), 473-476.
- 722
- 723 Finnoff, D., Strong, A., and Tschirhart, J. 2008. A bioeconomic model of cattle stock-  
724 ing on rangeland threatened by invasive plants and nitrogen deposition. *American Journal of*  
725 *Agricultural Economics*, 90(4):1074–1090.
- 726
- 727 Finnoff, D. and Tschirhart, J. 2008. Linking dynamic economic and ecological general equilibrium  
728 models. *Resource and Energy Economics*, 30:91–114.
- 729
- 730 Finnoff, D. and Tschirhart, J. 2009. Plant competition and exclusion with optimizing individuals.  
731 *Journal of Theoretical Biology*, 261:227–237.
- 732
- 733 Gillingham, K. and Huang P. 2018. Is abundant natural gas a bridge to a low-carbon future or a dead-  
734 end? *The Energy Journal*, 40(2), 1-26.
- 735
- 736 Gude, J.A., Garrott, R.A., Borkowski, J.J., and King, F. 2006. Prey risk allocation in a grazing  
ecosystem. *Ecological Applications*. 6(1): 285-298.
- 737
- 738 Gurney, W., and R. M. Nisbet. *Ecological dynamics*. Oxford University Press, 1998.
- 739
- 740 Hall, D., Rao, K. 1999. *Photosynthesis*. Cambridge University Press, Cambridge, United Kingdom,  
6th ed.
- 741
- 742 Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge (editors). 2011. Sagebrush ecosystem  
743 conservation and management: ecoregional assessment tools and models for the Wyoming Basins.  
744 Allen Press, Lawrence, KS. Hart, R. and Ashby, M. 1998. Grazing intensities, vegetation, and heifer  
745 gains: 55 years on shortgrass. *Journal of Range Management*, 51(4):392–398.
- 746
- 747 Hebblewhite, M. 2011. Effects of NGD on ungulates. In D. E. Naugle (Ed.), *NGD and wildlife*  
748 *conservation in western North America* (pp. 71–94). Washington, D.C.: Island Press.
- 749
- 750 Hironaka, R. and Freeze, B. 1992. Feedlot finishing of cattle (Rev. ed.). Ottawa, Ontario, Canada:  
*Agriculture Canada Publication 1591 (E)*.
- 751
- 752 Hobbs, N. T., Baker, D. L., Bear, G. D., and Bowden, D. C. 1996. Ungulate grazing in sagebrush  
grassland: Mechanisms of resource competition. *Ecological Applications*, 6(1), 200–217.
- 753
- 754 Holloran, M. J. 2005. *Greater sage-grouse (Centrocercus urophasianus) population response to*  
*natural gas field development in western Wyoming* (Dissertation Thesis). University of Wyoming.
- 755
- 756 Hussain, A. M. T., and Tschirhart, J. 2013. Economic/ecological tradeoffs among ecosystem services  
and biodiversity conservation. *Ecological Economics*, 93, 116–127.
- 757
- 758 Jablonski, K.E., Boone, R.B. and Meiman, P.J., 2018. An agent-based model of cattle grazing toxic  
Geyer's larkspur. *PloS One*, 13(3).

759  
760 Joskow, P. 2013. Natural gas: From shortages to abundance in the United States. *American Economic*  
761 *Review* 103(3): 338–343.

762 Kaiser, R. C. 2006. *Recruitment by greater sage-grouse in association with natural gas development*  
763 *in western Wyoming* (Dissertation Thesis). University of Wyoming.

764  
765 Kauffman, M.J., Meachem, J.E., Sawyer, H., Steingisser, A.Y., Rudd, W.J. and Ostlind, E. 2018. *Wild*  
766 *Migrations: Atlas of Wyoming's Ungulates*. Oregon State University Press, Corvallis, OR.

767  
768 Kim, S-H, Tschirhart, J., and Buskirk, S.W. 2007. Reconstructing past population processes with  
769 general equilibrium models: House mice in Kern County, California, 1926–1927. 209:235–248.

770  
771 Köchy, M. and Wilson, S.D. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91,  
772 385-395.

773  
774 Lambers, H., Chapin, F. S., III, Pons, T. L. (2006). *Plant Physiological Ecology*. New York: Springer.

775  
776 Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48(1), 25-  
777 34.

778  
779 Lyon, A. G., and Anderson, S. H. 2003. Potential gas development impacts on sage-grouse nest  
780 initiation and movement. *Wildlife Society Bulletin*, 31, 486–491.

781  
782 Mason, C.F. and Roberts, G. 2018. Price elasticity of supply and productivity: An analysis of natural  
783 gas wells in Wyoming. *Energy Journal, Special Issue*, 39, 79-100.

784  
785 Miller, T. E., Burns, J. H., Munguia, P., Walters, E. L., Kneitel, J. M., Richards, P. M., Buckley, H. L.  
786 2005. A critical review of twenty years' use of the resource ratio theory. *The American Naturalist*,  
787 165(4), 439–448.

788 National Wildlife Federation, and Wyoming Wildlife Federation. 2007. *Appeal presented to the*  
789 *Interior Board of Land appeals by the National Wildlife Federation and the Wyoming Wildlife*  
790 *Federation who appeal to the Bureau of Land Management regarding the Atlantic Rim Natural Gas*  
791 *Field Development Project record of decision*. Retrieved 2015-03-26, from  
792 [http://www.ourpubliclands.org/files/upload/Final SOR 7-20-07 NWF \\_WWF.pdf](http://www.ourpubliclands.org/files/upload/Final%20SOR%207-20-07%20NWF%20WWF.pdf)

793  
794 Naugle, D.E. (ed.) 2011. *Energy Development and Wildlife Conservation in Western North America*.  
795 Island Press A Well-Based Cost Function and the Economics of Exhaustible Resources: The Case of  
796 Natural Gas. Island Press, Washington, D.C.

797  
798 Northrup, J. M., and Wittemyer, G. 2013. Characterising the impacts of emerging NGD on wildlife,  
799 with an eye towards mitigation. *Ecology Letters*, 16, 112–125.

800  
801 Pennycuik C.J. 1979. Energy costs of locomotion and the concept of “foraging radius”. In: Sinclair  
802 ARE, Norton-Griffiths M (eds) *Serengeti: dynamics of an ecosystem*. University of Chicago Press,  
803 Chicago, 164–184.

804

805 Pfeiffer, M., Langan, L., Linstädter, A., Martens, C., Gaillard, C., Ruppert, J.C., Higgins, S.I., Mudongo,  
806 E.I., and Scheiter, S. 2019. Grazing and aridity reduce perennial grass abundance in semi-arid  
807 rangelands—Insights from a trait-based dynamic vegetation model. *Ecological Modelling*, 395:11-22.  
808

809 Powell, J. 2003. Distribution, habitat use patterns, and elk response to human disturbance in the Jack  
810 Marrow Hills, Wyoming. University of Wyoming. Laramie, Wyoming.  
811

812 Rowland, Mary M., Suring, Lowell H. and Wisdom, Michael J. 2010. Assessment of habitat threats to  
813 shrublands in the Great Basin: A case study. General Technical Report - Pacific Northwest Research  
814 Station, USDA Forest Service 2010 No.PNW-GTR-802(2) pp.673-685 ref.33.  
815

816 Sawyer, H., Nielson, R.M., Lindzey, F. and McDonald, L.L. 2006. Winter habitat selection of mule deer  
817 before and during development of a natural gas field. *Journal of Wildlife Management* 70:396-403.  
818

819 Solow, A. R., and Beet, A. R. 1998. On lumping species in food webs. *Ecology*, 79(6), 2013–2018.  
820

821 Sorensen, T. C., Mcloughlin, P. D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. 2008.  
822 Determining sustainable levels of cumulative effects for boreal caribou. *The Journal of Wildlife*  
823 *Management*, 72(4), 900–905.

824 Stephens, D. W., and Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.

825 Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist*, 125(6),  
826 827-852.  
827

828 Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by  
829 biodiversity in grassland ecosystems. *Nature*, 379, 718-720.  
830

831 Tschirhart, J. 2000. General equilibrium of an ecosystem. *Journal of Theoretical Biology*, 203(1), 13-32.  
832

833 Tschirhart, J. 2004. A new adaptive system approach to predator-prey modeling. *Ecological*  
834 *Modelling*, 176:255-276.  
835

836 Tschirhart, J. 2012. Biology as a source of non-convexities in ecological production functions.  
837 *Environmental and Resource Economics*. 51:189–213.  
838

839 U.S. Bureau of Land Management. 2007. *Record of decision: Environmental impact statement for the*  
840 *Atlantic Rim Natural Gas Field Development Project, Carbon County, WY*. (Tech. Rep.).

841 U.S. Energy Information Administration. Natural gas. Retrieved 2018-08-20, from  
842 <https://www.eia.gov/dnav/ng/hist/n9140us2A.htm>.

843 U.S. Energy Information Administration. 2018. U.S. Crude oil and natural gas proved reserves, year-  
844 end 2017. Nov. 2018, Washington, D.C.

845 U.S. Fish and Wildlife Service. 2003 Net Economic Values for Wildlife-Related Recreation in 2001.  
846 Addendum to the 2001 National Survey of Fishing, Hunting and Wildlife-Associated Recreation.  
847 Report 2001-3.

848 U.S. Fish and Wildlife Service. 2015a. *2015 endangered species act finding*. Retrieved 2016-02-16,  
849 from <http://www.fws.gov/greatersagegrouse/findings.php>

850 U.S. Fish and Wildlife Service. 2015b. *Greater sage-grouse*. Retrieved 2016-03-23, from  
851 <http://www.fws.gov/greatersagegrouse/>.  
852

853 Van Dyke, F., Fox, A., Harju, S.M., Dzialak, M.R., Hayden-Wing, L.D., and Winstead, J.B. 2012.  
854 Response of elk to habitat modification near natural gas development. *Environmental management*,  
855 50(5), 942-955.  
856

857 Walker, B. L., Naugle, D. E., and Doherty, K. E. 2007. Greater sage-grouse population response to  
858 NGD and habitat loss. *The Journal of Wildlife Management*, 71(8), 2644–2654.

859 Warren Resources, Inc., Annual Report. 2014. U.S. Securities and Exchange Commission, Form 10-  
860 K. Washington, D.C.

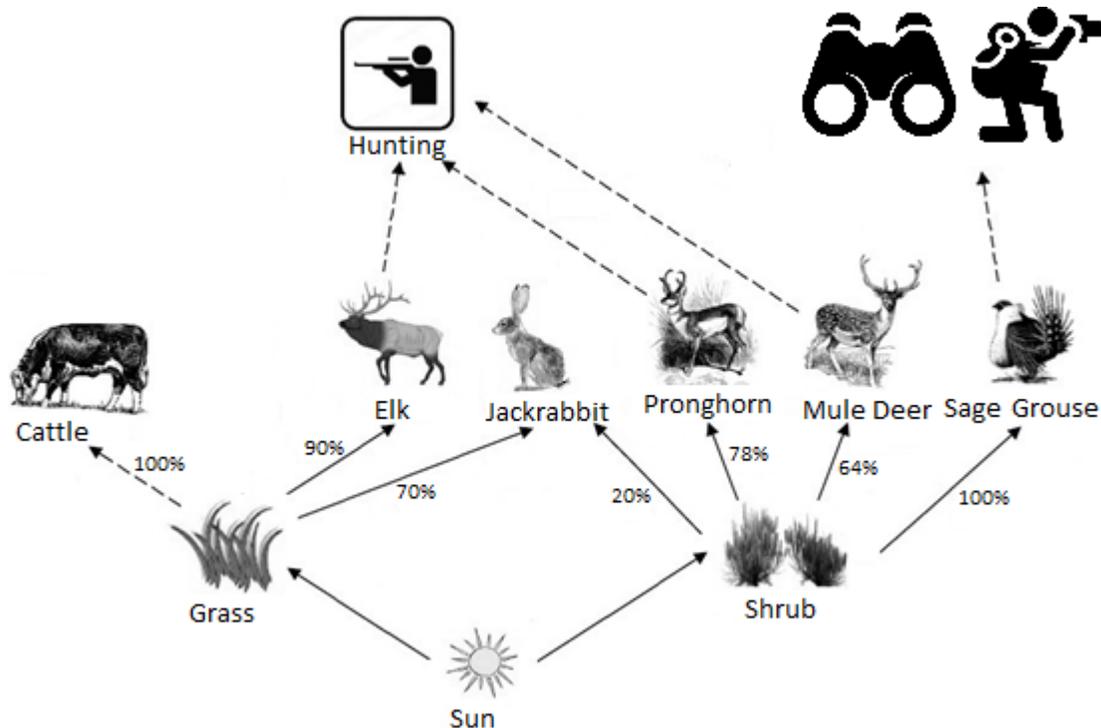
861 Wasser, S. K., Keim, J. L., Taper, M. L., and Lele, S. R. 2011. The influences of wolf predation,  
862 habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology*  
863 *and the Environment*, 9(10), 546–551.  
864

865 Water Resources Data Systems and Wyoming State Climate Office. 2008. Wyoming climate atlas:  
866 Solar radiation. Retrieved 28 May 2017: <http://www.wrds.uwyo.edu/sco/climateatlas/solar.html>.  
867

868 Wyoming Game and Fish Department. Annual reports of big and trophy game harvest and annual  
869 reports of small and upland game harvest. Retrieved October 16, 2014, from  
870 <https://wgfd.wyo.gov/Hunting/Harvest-Reports/>, 2014.

871 Xiao, H., Dee, L.E., Chadès, I., Peyrard, N., Sabbadin, R., Stringer, M. and McDonald-Madden, E.  
872 2018. Win-wins for biodiversity and ecosystem service conservation depend on the trophic levels of the  
873 species providing services. *Journal of Applied Ecology*, 55(5), 2160-2170.  
874

875 Yun, A.J., Lee, P.Y., Doux, J.D., Conley, B.R. 2006. A general theory of evolution based on energy  
876 efficiency: its implications for diseases. *Medical Hypotheses*, 66, 664–670.  
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 881 **Figure 1:** Grass (Gr) and shrubs (Sh) are the two plants and are composites of various species. (See  
 882 Solow and Beet (1998) on lumping species in food webs.) Grass is comprised of Idaho fescue  
 883 (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), bluebunch  
 884 wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), Thurber's needlegrass (*Achnatherum*  
 885 *thurberianum* (Piper) Barkworth), needle and thread (*Hesperostipa comata* (Trin. & Rupr.)  
 886 Barkworth), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Sandberg bluegrass (*Poa secunda* J.  
 887 Presl). Shrubs are comprised of *Artemisia tridentata* Nutt. from the Wyoming big sagebrush and the  
 888 mountain big sagebrush ecosystems (Davies, 2010, p. 462-4). Grass-eating herbivores are elk (*Cervus*  
 889 *elaphus*: El) and cattle (Ca). Shrub-eating herbivores are mule deer (Md), pronghorn (An), and sage  
 890 grouse (Sg). Jackrabbits (*Lepus townsendii* Bachman, 1839) are, both, grass- and shrub-eaters. The  
 891 arrows in the food web show the direction in which biomass (and thus energy) flows, and the  
 892 accompanying numbers show the percentage of a predator's diet coming from a prey species. For  
 893 example, grass makes up 90% of elk's diet. The dashed arrows show three categories of ecosystem  
 894 services: 1) pronghorn, mule-deer, and elk hunting, 2) cattle grazing on grass, and (3) existence value  
 895 of sage grouse.

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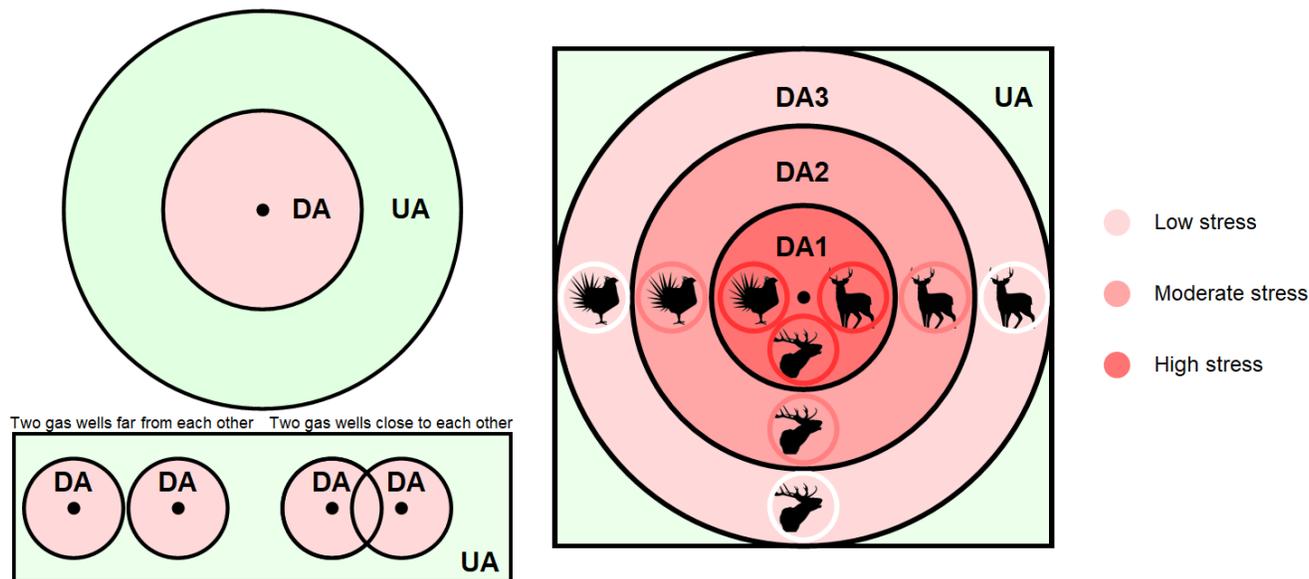
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Figure 2. Undisturbed and Disturbed Areas

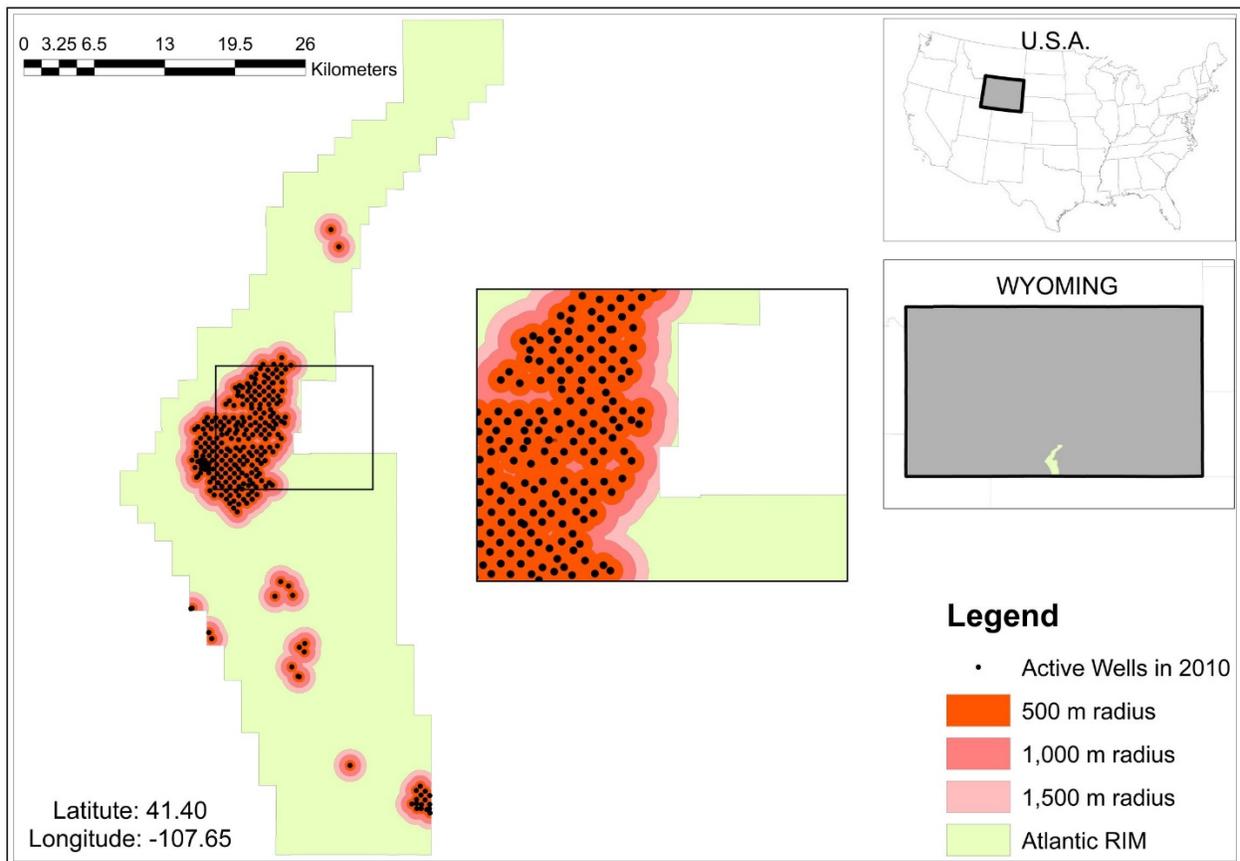


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906 **Figure 2:** The schematic on the left top side represents the elk, mule deer, and sage-grouse habitat loss  
907 or disturbed area (DA) around a well pad which is represented by a point. Depending on the radius of  
908 impact, the sizes of the DAs may vary according to the schematic on the right side. Mule deer, elk,  
909 and sage grouse experience the highest stress when foraging in the region labeled as DA1 (500 m), a  
910 moderate level of stress when foraging in DA2 (1,000 m), and the lowest stress when foraging in DA3  
911 (1,500 m). Any area not within a DA is the undisturbed area (UA). None of the animals experience  
912 stress when foraging in the UA. Other herbivores forage, respectively, in both DAs and UAs without  
913 experiencing stress. The schematic on the left bottom side shows that the total DA is the union of all  
914 DAs, and the total UA is the area of ARNG minus that union.

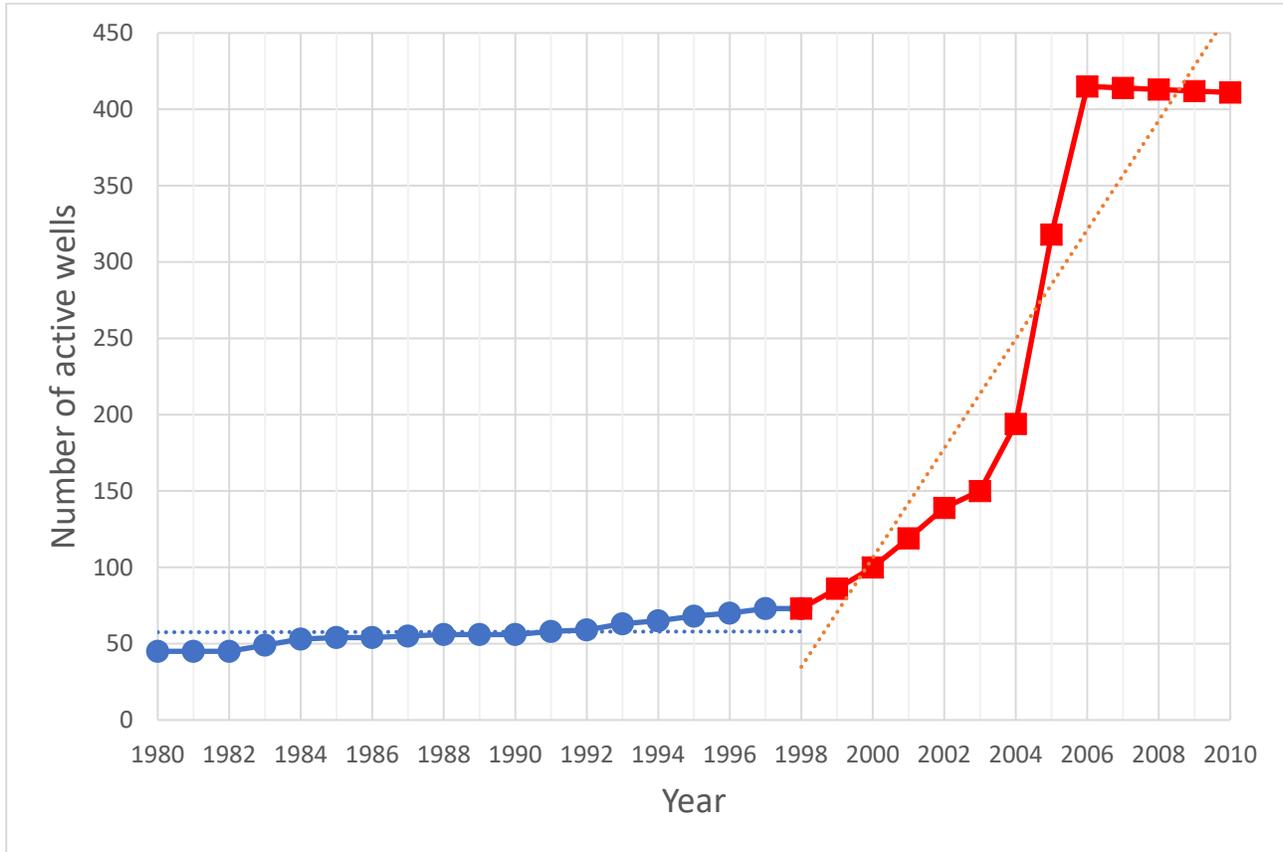
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Figure 3. ARNG Development



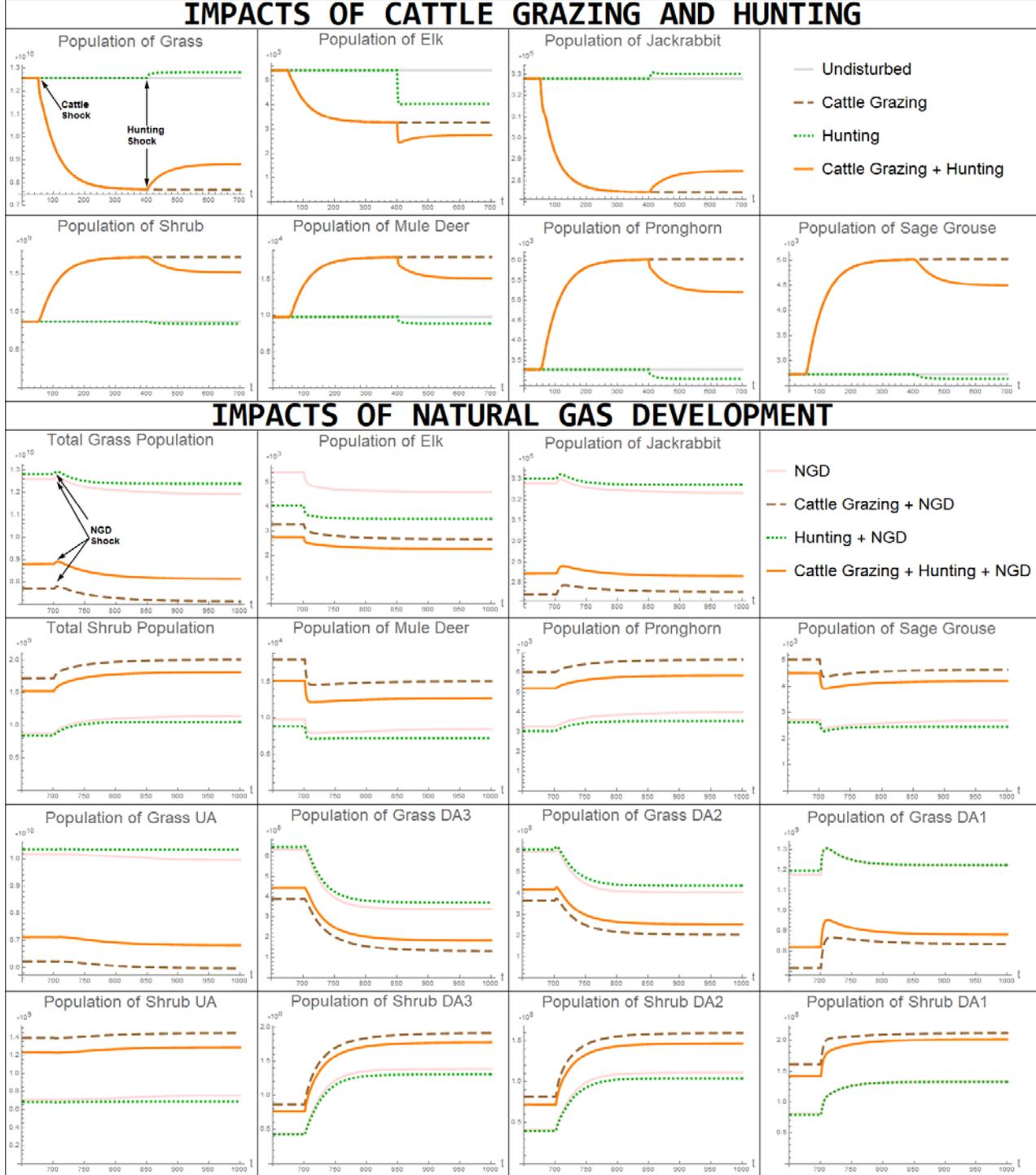
**Figure 3:** The upper right two maps show the location of Wyoming and the ARNG inside Wyoming. The green area represents the ARNG, the black dots represent the location of active natural-gas wells in 2010, and the peach-colored area represents the total DA when a radius of 500 meters, 1,000 meters, and 1,500 meters around each well is used.

Figure 4. The Total Number of Natural Gas Wells in the ARNG from 1980 to 2010



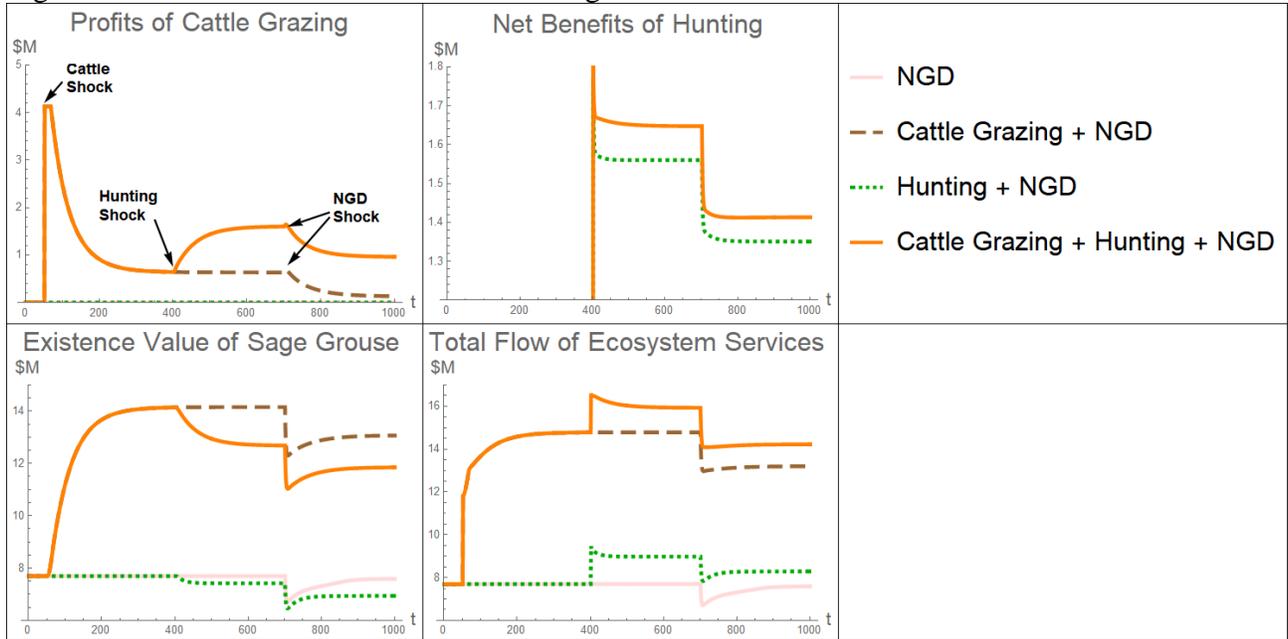
**Figure 4:** The solid line shows the number of active wells at the corresponding year in the ARNG region from 1980 to 2010. Importantly, even abandoned wells are relevant when measuring the impacts of NGD. The dashed line shows the piecewise linear trend of the total wells. Although it has generally been growing, the total number of active wells started increasing sharply in 1998. The first segment with circular markers shows a practically zero growth between 1980 and 1998, while the second section with square markers shows fast growth after 1998. Given this pattern, there have been approximately 15 years of major NGD in the region to date.

Figure 5. Plant and Animal Populations after the Introduction of Cattle Grazing, Hunting, and NGD



**Figure 5:** The graph shows the simulated time paths of populations of all species for four scenarios: (1) only NGD is introduced, (2) cattle grazing and then NGD are introduced, (3) hunting and then NGD are introduced, and (4) cattle grazing, hunting and NGD are introduced in that order. The graphs are split in two panels: prior to NGD and after NGD. The horizontal axes show time ( $t$ ) in years, the vertical axis shows the species' populations ( $n$ ). The plant populations after NGD are divided into three categories: the total ARNG population, the population in the UA, and the populations in DAs (DA1 is closest to the well pad; DA3 is the farthest from the well pad).

Figure 6. TDVES for the ARNG after Hunting and NGD



**Figure 6:** The graph shows the flow of ecosystem services value for four different scenarios: (1) where only NGD is introduced, (2) where cattle grazing is introduced and then NGD is introduced, (3) where only hunting is introduced and then NGD is introduced, and (4) where cattle grazing, hunting, and NGD are introduced in that order. The horizontal axes show time ( $t$ ) in years and the vertical axis shows the value in million dollars (\$M).

Table 1. List of Acronyms & Abbreviations used in the Manuscript

Acronym	Definition
NGD	Natural Gas Development
TDVES	Total Discounted Value of Ecosystem Services
GEEM	General Equilibrium Ecosystem Model
ARNG	Atlantic Rim Natural Gas development project
BLM	Bureau of Land Management
WGFD	Wyoming Game and Fish Department
EIS	Environmental Impact Statement
El	Elk
Md	Mule Deer
Sg	Sage Grouse
An	Pronghorn
Ca	Cattle
Jr	Jackrabbit
Gr	Grass
Sh	Shrub
FOC	First-Order Condition
MB	Predator-Prey Biomass-Balance
UA	Undisturbed Area
DA	Disturbed Area