

Potential futures for coastal wolves and their ecosystem services in Alaska, with implications for management of a social-ecological system

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S. Gilbert, T. Haynes, M. Lindberg, M. Kissling, D. Albert and D. Person contributed to analysis, and all co-authors contributed to ideas/framing, writing, and editing.

Keywords

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Abstract

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Carnivores across much of the world are declining, leading to loss of biodiversity as well as the ecosystem services carnivores provide. In 2020, the Alexander Archipelago (AA) wolf was petitioned for protection under the U.S. Endangered Species Act (ESA) for the third time in 30 years. Concerns included habitat alteration from industrial timber harvest and subsequent declines in prey (deer), human-caused mortality, climate change, and genetic inbreeding. However, the underlying biogeography and ecology of these wolves continues to suggest resiliency across the subspecies' range, even though local populations may go extinct. If local wolf populations go extinct, it will result in loss of their ecosystem services (e.g., interactions of wolves with their prey, which prevents over-browsing and protects carbon sequestration in soils and trees), which will likely have major consequences for the local social-ecological system. Here, we updated a model we constructed for the last ESA listing process (2015) to examine the dynamics of wolf and deer populations on Prince of Wales Island (the primary geographic focus of all three petitions) in response to future environmental and management scenarios developed with stakeholders. Further, we considered how changes in deer abundance impact predation services (prevention of over-browsing by deer). We found that wolf populations generally persisted over 30 years, but dropped below an effective population size of 50 wolves in 10%–98% of years simulated. Low wolf abundance resulted in higher deer abundance, which increased hunting opportunity, but also browsing damages (e.g., >30% of areas would be heavily browsed if wolves go extinct). Human harvest of wildlife was a key regulator of abundance and ecosystem services within the coastal rainforest social-ecological system; wolf abundance was most affected by wolf harvest regulations; and deer harvest restrictions increased wolf and deer abundances, but also greatly increased browsing impacts (>70% of areas heavily browsed if hunting ceased). Our findings support an integrated approach to management of this social-ecological system to ensure that the many ecosystem services humans depend on are valued, conserved and restored, including the cryptic predation services wolves have historically provided to the timber industry via reduced browsing pressure by deer.

Contribution to the field

Our work sheds new light on the potential futures of Alexander Archipelago Wolves in Southeast Alaska, and the key human and environmental variables in their social-ecological system that impact outcomes. We found that human harvest of both deer and wolves is critically important for determining the future, and that wolves can create considerable ecosystem services and disservices via predation on deer and subsequent changes to deer over-browsing of valuable conifers and deer hunting opportunities for people. We suggest an integrated approach to forest ecosystem and wildlife management that values the wide array of ecosystem services provided by the temperate rainforest.

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In review

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In review

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Abstract

Carnivores across much of the world are declining, leading to loss of biodiversity as well as the ecosystem services carnivores provide. In 2020, the Alexander Archipelago (AA) wolf was petitioned for protection under the U.S. Endangered Species Act (ESA) for the third time in 30 years. Concerns included habitat alteration from industrial timber harvest and subsequent declines in prey (deer), human-caused mortality, climate change, and genetic inbreeding. However, the underlying biogeography and ecology of these wolves continues to suggest resiliency across the subspecies' range, even though local populations may go extinct. If local wolf populations go extinct, it will result in loss of their ecosystem services (e.g., interactions of wolves with their prey, which prevents over-browsing and protects carbon sequestration in soils and trees), which will likely have major consequences for the local social-ecological system. Here, we updated a model we constructed for the last ESA listing process (2015) to examine the dynamics of wolf and deer populations on Prince of Wales Island (the primary geographic focus of all three petitions) in response to future environmental and management scenarios developed with stakeholders. Further, we considered how changes in deer abundance impact predation services (prevention of over-browsing by deer). We found that wolf populations generally persisted over 30 years, but dropped below an effective population size of 50 wolves in 10%–98% of years simulated. Low wolf abundance resulted in higher deer abundance, which increased hunting opportunity, but also browsing damages (e.g., >30% of areas would be heavily browsed if wolves go extinct). Human harvest of wildlife was a key regulator of abundance and ecosystem services within the coastal rainforest social-ecological system; wolf abundance was most affected by wolf harvest regulations; and deer harvest restrictions increased wolf and deer abundances, but also greatly increased browsing impacts (>70% of areas heavily browsed if hunting ceased). Our findings support an integrated approach to management of this social-ecological system to ensure that the many ecosystem services humans depend on are valued, conserved and restored, including the cryptic predation services wolves have historically provided to the timber industry via reduced browsing pressure by deer.

Keywords: Alaska; U.S. Endangered Species Act; predator-prey interaction; Predation services; Alexander Archipelago Wolf; *Canis lupus ligoni*; Sitka Blacktail Deer; *Odocoileus hemionus sitkensis*

Introduction

Most top carnivore species around the world are in decline (Ripple et al. 2014), with corresponding losses not only of biodiversity but also of “predation services” that regulate the abundance and behavior of prey species that have net negative effects on people and ecosystems (Braczkowski et al. 2018; O'Bryan et al. 2018; Gilbert, Carter, and Naidoo 2021). However, in many parts of Europe and North America, large carnivore populations are making a comeback due to increased legal protection, and in some cases increasing tolerance, for predatory wildlife (Manfredo, Teel, et al. 2021, Treves et al. 2013, Dressel et al. 2015), leading to heated debate about whether carnivores should be lethally managed to reduce damages, enjoy continued

66 protection under laws such as the U.S. Endangered Species Act (ESA), or be actively re-
67 introduced to new areas (Manfredo, Berl, et al. 2021). These divergent desires regarding
68 carnivore recovery are likely due in part to the fact that those who experience or perceive
69 negative effects of predation (e.g., some ranchers and hunters) are not the same people that
70 experience or perceive the positive services of predation (e.g., environmentalists, wildlife
71 viewers, range and forest land managers; S. Gilbert, Carter, and Naidoo 2021; Manfredo, Berl, et
72 al. 2021).

73 In contrast to trends on the mainland of North America, wolves in some portions of the
74 coastal temperate rainforests of Alaska (*Canis lupus ligoni*) have declined from historical levels
75 due to many of the same factors that are driving global carnivore declines: reductions in prey
76 base following habitat alteration and human harvest (Person and Brinkman 2013, S. L. Gilbert et
77 al. 2015). As a result, the Alexander Archipelago (AA) wolf has been petitioned for listing under
78 the ESA three times in the past 30 years, including a recent petition filed in 2020 that is currently
79 under 12-month review (USFWS 2021), with concerns focused on the population of wolves
80 living on Prince of Wales Island. Over the past century, timber harvest and associated
81 development has dramatically altered coastal temperate rainforests of the Pacific Northwest of
82 North America (DellaSala 2011), a highly productive region that provides many ecosystem
83 services (Brant et al. 2014). As a result, the coastal temperate rainforest has become a focus of
84 controversy for both the timber industry and conservation interests, with AA wolves one of the
85 most contentious species. As is common with many wolf populations (Musiani & Paquet 2004),
86 public perceptions of AA wolves range widely, from wolves being undesirable due to negative
87 cultural stereotypes and real and perceived competition with deer hunters (Brinkman et al. 2007,
88 Liberg et al. 2012, Person and Brinkman 2013, Pohja-Mykrä and Kurki 2014, Bradley et al.
89 2015), to high conservation concern for the persistence of AA wolves in the face of various
90 impacts, including a reduction in prey (Person and Brinkman 2013) and potential genetic
91 inbreeding following heavy human harvest (Center for Biological Diversity, Alaska Rainforest
92 Defenders, and Defenders of Wildlife 2020).

93 While the causes of AA wolf declines are varied, most pathways directly or indirectly
94 lead back to human actions driven by timber harvest. The impacts to deer habitat have
95 manifested through large scale old-growth logging and subsequent forest succession. Massive
96 old-growth logging in the last decades of the 20th century and subsequent forest succession to
97 lower-productivity, older second-growth stages (Alaback et al. 1982) has reduced the habitat
98 carrying capacity for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), the primary food
99 source for AA wolves. Timber harvest also increases the density of road networks, providing
100 greater access for wolf hunting and trapping (Person and Russell 2008, Person and Logan 2012;
101 Fig. 1). In addition, industrial logging compacts soils, which can reduce seedling recruitment and
102 forage quality by disrupting plant-soil-microbe feedbacks. Given strong links to deer and wolf
103 populations, high levels of timber harvest likely reduce the long-term viability of wolf
104 populations and the stability of predator-prey dynamics and ecosystem resiliency in Southeast
105 Alaska (Person et al. 1996, Person and Brinkman 2013, Roffler et al. 2018).

106 Prince of Wales (POW) and adjacent outlying islands support a significant percentage of
107 the wolves in Southeast Alaska (Person et al 1996), which has declined sharply in recent years
108 (Alaska Department of Fish and Game 2015a, 2020). In 1993, a petition was filed for protection
109 of the AA wolf under the ESA, but ultimately the U.S. Fish and Wildlife Service (USFWS)

determined that listing was not warranted because declines would stop within an acceptable level (62 Federal Register 46710, September 4, 1997). In 2011, another ESA petition was filed, citing the same primary threats but adding climate change and inadequate harvest regulatory mechanisms as additional pressures (Center for Biological Diversity and Greenpeace 2011).

At the request of the USFWS, we created a population model in 2014-2015 for wolves on POW and the surrounding islands to inform the listing decision. The purpose of our analysis was to develop a model best representing our current understanding of predator-prey dynamics on POW, then assess the effects of major stressors on future wolf abundance. We evaluated six possible scenarios spanning a range of likely conditions for future timber harvest, silvicultural treatments that affect forest succession, deer abundance, road building and closures, and wolf harvest regulations. We also conducted sensitivity analyses to measure the relative influence of these factors on wolf and deer abundances. While our model identified a number of scenarios in which wolves on POW could decline to low levels in the future, the USFWS declined to list AA wolves in their 12-month finding (2015), because the AA wolf was not deemed threatened through all or a portion of its range (all of Southeast Alaska and northern British Columbia), and the POW population was not deemed ecologically or genetically unique enough to qualify as a distinct population segment under the ESA (USFWS 2016). The current petition, rather than focusing on the POW population, requests that AA wolves throughout Southeast Alaska be listed as a threatened, distinct population segment within the broader sub-species range in coastal Canada and Alaska. However, POW's wolves are again at the heart of the petition, in part because recent intensive harvests wolf harvest in recent years may have led to inbreeding depression (Zarn 2019).

Regardless of the outcome of the current ESA listing decision, wolves on POW may go functionally or completely extinct, with potential for profound but poorly recognized impacts to the social-ecological system (the ESA does not require consideration of economic impacts, even if the wolves were listed). What would a "world without wolves" look like on POW? AA wolves clearly are valued by some residents and non-residents, and provide a number of "predation services and disservices" via their consumption of deer, the only significant ungulate herbivore in the ecosystem.

Fortunately, a wolf-free comparison is available for consideration on Haida Gwaii, the large island complex just south of POW in British Columbia. Sitka black-tailed deer are not native to Haida Gwaii, but were introduced to the northern portion of the archipelago ~100 years ago, after which they spread rapidly across much of the archipelago. They currently sustain densities of ~15-35 deer/km² (or almost 40 deer/square mile). Despite having drastically depleted understory biomass and impacted soils (Le Saout et al. 2014; Gaston 2007), deer remain at high densities and continue to suppress plant recruitment and growth, potentially by consuming lichens that blow down from old-growth forest canopies in fall and winter, when deer would otherwise be nutritionally limited by terrestrial plant biomass (Le Saout et al. 2014). Palatable plants, such as huckleberry and commercial and culturally important tree species such as western red cedar (*Thuja plicata*), have been almost entirely removed by browsing where deer are present. Even less palatable conifer species, such as Sitka spruce (*Picea sitchensis*), exhibit stunted growth by up to two decades by browsing pressure compared to deer-free areas, until they are finally able to reach a height where they "escape" browsing (Bachand et al. 2014).

Browsing disservices not only damage the forestry industry by delaying timber rotations for high-value cedar and other conifers, but also impact Haida and Tlingit tribal members living on POW who value cedar and huckleberry for their traditional uses (Norton 1981; Moss 2004; Benner et al. 2021). Over-browsing also impacts ecosystem resiliency and the net forest carbon (C) balance. Browsing can negatively impact habitat availability, along with plant, bird and invertebrate biodiversity (Maillard et al. 2021), and soil function. Preferential consumption of higher-quality (lower C to nitrogen) plant litter reduces microbial productivity the delivery of critical nutrients, such as nitrogen (Maillard et al. 2021). However, a more abundant deer population also would provide more hunting opportunities, and phosphorus, to plants. Nutrient limitation can also stimulate heterotrophic respiration, reducing net forest carbon sequestration. Deer are a regionally prized game species for both sport and subsistence hunters (Colson et al. 2013; Brinkman et al. 2009). More abundant deer can also increase soil C persistence through soil compaction. Wolves therefore exert both a predation disservice, by reducing hunting opportunities, and a predation service, by increasing the abundance of desirable conifer species and provisioning other ecosystem benefits that are difficult to quantify and often overlooked (Maillard et al. 2021; Martin et al. 2020). Critically, wolves prey on deer wherever they co-occur within the remote, rugged landscapes of the temperate rainforest, whereas human hunters have a strong preference for landscapes with easy boat and road access and high sightability (Brinkman et al. 2009). Therefore, even if deer hunting regulations were drastically loosened or the number of hunters increased greatly, it is unlikely that human hunting could provide an equivalent deer regulatory service over the entirety of the study area. For example, despite extremely generous hunting regulations on wolf-free Haida Gwaii (>15 deer per hunter per year), hunters are unable to regulate deer numbers and negative impacts of deer persist. Indeed, the Canadian government recently spent millions of dollars hiring professional hunters from New Zealand to remove deer from several small islands that are part of the Haida Gwaii archipelago to produce deer-free biodiversity refuges (Anthony, 2019).

Here, we update our 2015 model to consider loss of predation services, via increased browsing pressure, and discuss the implications for AA wolf conservation and social-ecological feedbacks on POW and elsewhere.

Materials and Methods

Study Area

We focus on the POW region (Fig. 2) because it has historically supported a large, and relatively isolated (Weckworth et al. 2005, Breed 2007, Cronin et al. 2015, Zarn 2019) portion of the AA wolf population in Southeast Alaska (Person et al. 1996) and has a high concentration of stressors that could lead to local extinction, including intensive timber harvest, road density, and easy boat access (Person 2001). This study region was also a focal area in the status assessment conducted in 2015 by the USFWS for consideration of listing of AA wolves under the Endangered Species Act (Gilbert et al. 2015). The POW region (Fig. 2) has a mean annual precipitation of >300 cm which produces a diversity of temperate rainforest habitats including old-growth forest types, alpine and subalpine vegetation above ~400 m, and muskeg heaths (Farmer and Kirchhoff 2007, Alaback and Saunders 2013). Industrial timber harvest has dramatically altered old-growth forests and removed disproportionate amounts of commercially

valuable forest from the study area relative to the region as a whole (Albert and Schoen 2013). Albert and Schoen (2007) estimate that 40% of the productive forest land on North POW and 9% on South POW has been logged.

The diet of POW wolves is diverse compared to their continental counterparts, and includes a greater marine component, although deer remain the most important prey item (Szepanski et al. 1999). The primary drivers of deer population dynamics in Southeast Alaska include winter severity, habitat quality, predation by wild carnivores, and harvest by humans (Fig. 1). During winter, deep snow impacts deer by increasing the cost of movement (Parker et al. 1984), burying forage (Parker et al. 1999, White et al. 2009), reducing landscape connectivity, foraging efficiency, and habitat carrying capacity (Gilbert et al. 2017, Kirchhoff 1994, Parker et al. 1999, Hanley et al. 2012). Consequently, deer populations can decline sharply in or following severe winters (Farmer et al. 2006, Person et al. 2009, Brinkman et al. 2011, Gilbert et al. 2020).

Industrial timber harvest has diminished habitat quality for deer by converting structurally diverse old-growth forests to even-aged stands throughout much of Southeast Alaska, and especially in the southern portions of the Alexander Archipelago, including POW. Young and old second-growth has been associated with increased mortality risk for deer due to increased hunting and malnutrition (Farmer et al. 2006, Person et al. 2009) and old second-growth landscapes have lowest deer densities after consecutive severe winters (Brinkman et al. 2011). Landscapes dominated by second-growth habitats are likely to have lower deer populations, which in turn negatively affects wolf densities.

In addition to acting as primary prey of wolves, deer are also an important resource for both humans and bears (Fig.1). Much of the deer harvest in Southeast Alaska is concentrated on POW due to the ease of access on the widespread road system created by timber harvest, relatively high deer densities, and liberal harvest regulations (Brinkman et al. 2009). In addition to human harvest, deer populations experience mortality due to predation on fawns occasionally by eagles (Gilbert 2016) and more frequently by black bears (*Ursus americanus*; Gilbert 2015).

Modeling approach

We based our model on a pre-existing population model for wolves on POW and surrounding small islands. This model was created by Person and Bowyer (1997) and refined in 2001 (Person 2001) henceforth the “2001 model”). The 2001 model used data specific to wolves in the study area when available, as well as data and relationships from studies of wolves and deer in other ecosystems when data specific to POW were not available. The 2001 model exhibited good performance for describing population dynamics when validated on other systems with more complete data, such as deer at the George Reserve, wolves on Coronation Island, and wolves and moose at Isle Royale (Person et al. 2001). We updated the 2001 model using new data from Southeast Alaska to better parameterize variables (Table S1).

Using our updated model, we simulated the effects of a range of plausible environmental changes on wolf abundance. The basic structure of the model includes the major factors expected to influence future wolf abundance: changes to deer carrying capacity, projections of winter severity, and harvest rates of wolves by humans. Secondary drivers are considerably more complex (Fig. 1), resulting in relationships that are either one-way, or involve density-dependent feedback loops. We describe in detail the equations used to structure the wolf population model,

as well as updates made to the model's parameters in Appendix 1, and list new data sources in Table A1. Below, we describe the basic model structures.

We modeled wolf population dynamics as a cumulative sum of dynamics of 31 hypothetical, spatially-explicit, contiguous wolf "packs" (Fig. 2). Each pack's home-range was represented by a polygon with a mean size of 303 km² (SD = 87), which is in line with empirical estimates of wolf home-range sizes, ranging from 260 km² (SE = 48; Person 2001) to 535 km² (Alaska Department of Fish and Game 2015b). Although we use the term "packs" to describe wolves in each polygon, wolves in a polygon do not have to be organized into a single pack, although the dynamics of all packs in a given polygon are linked. We recognize that wolf pack territories and home ranges are dynamic and our pack areas are modeled as static. We used the same pack polygon boundaries established by Person (2001) and assumed a closed population of wolves in the study area, although we allowed wolves to disperse among all pack polygons without geographic restrictions. Dispersal of wolves among packs allowed packs to be more realistically dynamic in terms of recovery from local extinction, because new wolves could colonize from other packs. Demographic rates for wolves in our model, particularly recruitment and mortality, are regulated by the ratio of deer to wolf abundance in pack areas. In addition, those demographic rates are given wide distributions such that they can accommodate hypothetical changes in numbers of packs within pack areas. For example, if the ratio of deer to wolves is high, recruitment to wolves also can be high. In this example, our model would accommodate either a single pack with a large litter of pups, or a situation in which a second breeding pair establish a territory within the pack area, although such social dynamics are not modeled explicitly. We allow a 2-year time lag for the effects of deer/wolf ratios to be fully manifested within a pack to account for asynchrony between deer and wolves. A limitation of our model is it does not model the distribution of those resources at a finer resolution than the pack area. For example, if high quality habitat for deer is concentrated along a border between pack areas, a small change in area boundaries could have a large effect on which group sequesters those deer. Consequently, our model likely underestimates the potential variation in the ratio of prey to wolves and in wolf-deer predator-prey dynamics.

Model structure

Within each wolf pack area i , annual wolf numbers at time t are described using the formula:

$$P_{t+1(i)} = P_{t(i)} + R_{Pt(i)} - T_{Pt(i)} - D_{Pt(i)} - M_{t(i)} + I_{t(i)}$$

where $P_{t(i)}$ is the size of the wolf pack prior to parturition in pack area i , $R_{t(i)}$ is recruitment, $T_{t(i)}$ is wolves harvested, $D_{t(i)}$ is dispersal, $M_{t(i)}$ is natural mortality, and $I_{t(i)}$ is immigration from other packs. Recruitment, natural mortality, and dispersal probability were modeled as density dependent, based on the ratio of deer available to deer consumed for each wolf pack (Appendix A, Equations A.7, A.9 and A.10). We considered natural mortality and dispersal to be compensatory with mortality from human harvest (i.e., human harvest reduces rates of natural mortality and dispersal; Person & Bowyer 1997). Human harvest of wolves for each pack was determined based on road density and distance via ocean from the nearest human settlement (Person & Russell 2008; Appendix A Eq. A.8). Individual wolf packs affect overall wolf pack dynamics by contributing dispersing wolves to a population wide "dispersal pool" in a density-dependent manner. Wolves that enter the dispersal pool could colonize vacant pack areas. We

modified the 2001 model so that if wolves in the dispersal pool did not colonize a vacant pack area in year t , individuals in this pool had an annual survival probability of 0.34 (SE = 0.17) (Person and Russell 2008).

The deer sub-model is a component of the wolf population model that represents prey resource dynamics in the pack areas (details in Appendix A). The deer population ($U_{t(i)}$) at time t was calculated as:

$$U_{t+1(i)} = U_{t(i)} + R_{ut(i)} - BA_{t(i)} - CP_{at(i)} - H_{t(i)}$$

Where $R_{ut(i)}$ is recruitment into the deer population in pack area i , $BA_{t(i)}$ is predation mortality of adult deer by black bears, $CP_{at(i)}$ is predation mortality of deer by wolves, and $H_{t(i)}$ is harvest mortality from human hunting. C , the per-capita wolf predation rate (15 deer/wolf/year) was based on a wolf diet estimate for POW from a stable isotope analysis (Szepanski et al. 1999) and thus represents a conservative minimum number of deer killed, given that wolves do not necessarily consume the entire deer carcass. $P_{at(i)}$ is the average of spring and fall population sizes of wolves in year t . Similar to the wolf model, the deer model was density-dependent. Recruitment scaled with proximity of the deer population in pack area i to the carrying capacity of deer in that pack area (Supplementary Information 1, Equation 2), and was assumed to have failed completely if a severe winter occurred, as severe winters impact fawns far more than adults (Gilbert et al. 2021). Predation of fawns by black bears was also modeled as density-dependent, with the percentage of compensatory mortality increasing as the deer population approached carrying capacity, K (Supplementary Information 1, Equation 3). We predicted deer carrying capacity in each pack area from the deer habitat capability index (deer HCI; originally developed by Suring et al. 1993, and updated by an interagency deer team intermittently), which estimates the maximum number of deer that can be nutritionally supported during winter in a specified area (US Forest Service 2008). We treated adult deer mortality due to hunting, and predation by black bears and wolves as completely additive. Hunting mortality on deer was a function of road length, based on a published regression relationship between road length and reported harvest (Person & Bowyer 1997; Supplementary Information 1, Equation 5), although importantly this equation is not sex or age specific, and specifies no maximum capacity was specified for hunting in terms of demand or number of total hunters and their effort, other than the total population of deer available in a WAA. Person and Bowyer (1997) found no difference in performance of more complex sex- and age-structured models versus an unstructured model, so we retained their equation. Potential biases produced by this equation are over-estimation of deer hunters' ability to harvest deer and resulting hunting services and wolf disservices, as real-world harvest is heavily male-biased.

Predation services and disservices via deer reductions were based on impacts to cedar recruitment and delays in conifer regrowth on Haida Gwaii, and predicted levels of hunting (see above for potential biases in hunting). However, because the deer HCI model generally predicts relatively low deer densities, well below the 30 deer/km² density at which severe browse impacts to conifers were observed on Haida Gwaii, and is a predictor of habitat value to deer rather than absolute deer densities, we instead assumed that deer browse impacts would occur if deer density exceeded 90% of carrying capacity (K).

Scenario development

We developed 6 scenarios for analysis that spanned a range of possible future conditions on POW. The conditions for each scenario were based on proposed or planned land use and resource management actions, as well as on future climate possibilities for the region, downscaled from global climate models (i.e., winter severity frequency, Supplementary Information 1). We developed the scenarios during a technical model review workshop (Anchorage, AK, March 18–19, 2015) that included participants from key management agencies, along with technical experts in population modeling, spatial analysis, and wolf ecology.

Scenarios included likely future changes to timber harvest, road building or closures (i.e., decommissioning), effects of climate change on frequency of severe winters, and wolf harvest regulations. We considered changes to vegetation based on 5 potential timber harvest conditions: 1) no future timber harvest after 2014 (i.e., forest successional change only); 2) a transition to harvest of second-growth forest on Tongass National Forest lands (i.e. the young growth transition currently in planning by the U.S. Forest Service); 3) continued harvest of old-growth at the rates observed from 2008–2014; 4) increased harvest of old-growth forest at the rates observed from 1995–2000; and 5) maximum harvest of old-growth forest allowable under the 2008 Tongass Land Management Plan. We also varied the rate of future timber harvest assumed to occur on non-federal lands among these alternatives. Details and assumptions associated with these possible future vegetation conditions are included in Supplementary Information 2.

We considered 5 alternative conditions for road construction and decommission: 1) no change in total road length from 2014 levels; 2) road decommissioning at levels in current management plan (i.e., -2.2 % total road length, implemented during 2015–2025; US Forest Service 2009); 3) road decommissioning at increased levels (i.e., -28.7% total road length, implemented during 2015–2025); 4) road decommissioning at maximum levels (i.e. -32% total road length, implemented during 2015–2025); and 5) road construction necessary to access new old-growth harvest areas if the maximum old-growth harvest scenario takes place (i.e., 30% increase in total road length). We calculated road construction necessary to access new old-growth based on a regression relationship between existing total road length and acres of timber harvest in the wolf pack areas (United States Forest Service 2008). We used the resulting slope (i.e., regression coefficient, $\beta = 0.0385$, $SE = 0.0026$, $R^2 = 0.88$), which specifies 0.0385 km of road construction per hectare of new logging.

Wolf harvest regulations included in the scenarios ranged from complete closure of regulated harvest (0% reported harvest) to closure of harvest within a harvest season if reported harvest exceeded a fixed percentage (20% and 30%) of the previous fall population (i.e., a harvest “cap”). In addition, Person and Russell (2008) found that 13 of 31 (42%) wolves harvested by humans were not reported. As a result, we use regression relationships to predict reported harvest based on road density and distance to nearest town via ocean (see Supplementary Information 1, equation 8), then multiplied the result by an unreported harvest scalar of 1.72, equivalent to total harvest ($n = 31$) divided by reported harvest ($n = 18$), then applied a harvest cap to the reported portion of the predicted harvest for each pack if the cap threshold for a scenario was exceeded at the population level.

Combining these factors, along with possible future frequencies of severe winters (Supplementary Information 1), we created six scenarios with input from workshop participants for evaluation (Table 1). Across scenarios, we hypothesized that Scenario A would be most favorable for wolf abundance and resilience of the predator-prey community, Scenario B would

be the most likely under current agency policy, Scenario E would be least favorable for wolf abundance, and Scenarios C and D are intermediates between A and E in terms of favorability for wolves. We also included a No New Action scenario, which represented ongoing changes in forest succession and habitat values from past logging, with no additional change or management action in the future (Table 1). We chose a 30-year timeframe (2015 to 2045) for model simulations because it encompassed enough years for the population dynamics of long-lived animals such as deer and wolves to stabilize and respond to environmental change but was short enough to minimize uncertainty associated with future management, climate, and socioeconomics. For each scenario, we conducted 1,000 30-year simulations of the wolf-deer model.

Table 1. Description of scenarios evaluated using the wolf population model.

Scenario	Vegetation	Roads	Wolf harvest	Predicted frequency of severe winter
No New Action	Natural succession only	No change	20% harvest cap	Average
Scenario A	Natural succession only	Planned decommission	No legal harvest	Low
Scenario B	Young growth transition	Planned decommission	20% harvest cap	Average
Scenario C	Continued harvest of old growth	No change	20% harvest cap	Average
Scenario D	Maximum harvest of old growth	Road construction	30% harvest cap	High
Scenario E	Increased harvest of old growth	No change	30% harvest cap	High

Sensitivity analysis

To isolate how scenarios are affected by changes to vegetation, road length, frequency of severe winters, and wolf harvest regulations, we perturbed each of these variables separately across the range of values found in the scenarios, while holding all other variables at Scenario B values. As with the primary scenarios analysis, for each parameter perturbation, we conducted 1,000 30-year simulations of the wolf-deer model. We also tested model sensitivity to wolf diet composition, examining wolf diets comprised of 15 deer/wolf/year used in scenarios (i.e., 45% deer in the diet) versus 9.5 deer/wolf/year (i.e. 28% deer in the diet), 20.5 deer/wolf/year (i.e., 60% deer in the diet), or 26 deer/wolf/year (i.e. 77% deer in the diet; the value used by Person 1996). Finally, we explored the effects of changing deer harvest in the study area, by considering the most extreme alternative: no deer harvest. We included this condition because the model could not realistically quantify the effects of different levels of deer harvest in its current form (i.e., a model with a single sex and adult age class). We included a wolf harvest perturbation of no cap on harvest (i.e., harvest depends on environmental predictors only), because ADFG shifted harvest regulations to a non-capped system in recent years, resulting in high harvest rates (ADFG 2021). As with scenario results, we present results of sensitivity analysis as a percent change in abundance over 30 years from 2014 levels (i.e., total change by 2045) and base interpretation on relative comparisons.

Quasi-extinction calculations

We investigated effects of 6 possible scenarios on the probability that wolf abundance would fall below a quasi-extinction (QE) threshold (i.e., abundance that is so low that the population is at significant risk of extinction). The 50-500 rule is commonly used in conservation genetics to determine the QE threshold (Franklin 1980). This rule suggests that an effective population size (N_e ; number of animals contributing genes to the next generation) of at least 50 is needed for short-term population viability, whereas an N_e of 500 or more is needed to ensure long-term viability (Laikre et al. 2016). Among wolves, only a fraction of the population breeds, so that N_e is lower than total abundance, N (Aspi et al. 2006, Laikre et al. 2016). We therefore assume a ratio of N_e/N of 0.42 (i.e., only 42% of wolves pass on genes to the next generation), as has been recorded for Finnish wolves, an analogously small and isolated population (Aspi et al. 2006, Laikre et al. 2016). Using this ratio, we calculated that to achieve $N_e = 50$, an $N = 119$ was needed, whereas to achieve $N_e = 500$, N must equal 1,190 wolves, far beyond likely historical wolf abundance on POW. We calculated the percentage of years under each scenario that wolf abundance will drop below 119 wolves to assess how frequently the POW wolf population would drop below the QE threshold. We chose this approach, rather than simply counting number of population realizations where $N < QE$, because the low initial starting size of the population (i.e., 89 wolves) ensures that almost all populations start below the QE threshold.

Results

Scenario development

Between 1995 and 2015, the composition of forests logged in the study area shifted from primarily young growth to primarily old second-growth, despite continued but slowed harvest of remaining old-growth forests (Table S3). These changes represent a decline of approximately 13% in carrying capacity (K) for deer from 1995 to 2015. By 2045, we project that 100%, 86%, 89%, 90%, and 93% of cut forests will have transitioned to old second-growth in No New Action, Scenario A, Scenario B, Scenario C, Scenario D, and Scenario E, respectively (Table S3). Under the 'No New Action' scenario and Scenario A, we estimated an additional decline of 6% in deer K by 2045, with larger projected declines under Scenario B (-9%), Scenario C (-11%), Scenario D (-14%) and Scenario E (-17%).

Scenario outcomes

From the low, empirically estimated starting abundance of 89 wolves in fall of 2014 (95% CI = 50, 159; (Alaska Department of Fish and Game 2015a), the projected wolf population in 2045 increased in four scenarios and decreased in two (range: -35 to 284%) and deer abundance declined across all scenarios (range: -9% to -36%; Table 2, Figs. 3 and 4). Across scenarios, wolf abundance dropped below an effective population size of 50 wolves in 10%–98% of years simulated. Deer browsing damage to conifers varied across scenarios and through time, with 0–16% of wolf home ranges impacted by heavy browsing by 2045, whereas deer hunting opportunity declined across scenarios from 19–60% (Table 2), although only some of this loss is attributable to wolves (see sensitivity analysis, below), because deer abundance declined in general due to dwindling habitat carrying capacity.

Table 2. Modeled changes from 2015–2045 in spring abundance of wolves, deer, and predation services (percentage of wolf pack areas exposed to heavy browsing in 2045) and disservices (change in hunting opportunities for deer) under future scenarios. Populations with fewer than 119 wolves drop below the quasi-extinction (QE) threshold. Estimates are shown with 95 % confidence intervals.

Scenario	Median wolf abundance	Median % change wolf	Median % change deer	Median % change hunt	Percent wolf ranges browsed
No New Action	134 (48, 184)	65 (-41, 127)	-10 (-25, -1)	-30 (-45, -14)	6 (0, 22)
Scenario A	311 (261, 358)	284 (222, 342)	-36 (-51, -22)	-6 (-8, -4)	0 (0, 0)
Scenario B	132 (47, 180)	63 (-42, 122)	-11 (-25, -2)	-30 (-5, -17)	10 (0, 23)
Scenario C	132 (46, 180)	64 (-43, 125)	-12 (-26, -4)	-31 (-46, -20)	10 (0, 23)
Scenario D	58 (8, 109)	-28 (-90, 35)	-9 (-22, -5)	-27 (-41, -21)	16 (3, 29)
Scenario E	53 (9, 98)	-35 (-89, 21)	-17 (-30, -14)	-19 (-37, -14)	13 (3, 23)

Scenario A resulted in the largest increase in wolf abundance (284%, 95% CI = 222, 342), which included no further timber harvest (i.e., natural succession only from 2015 onwards), planned decommission of roads, a low future frequency of severe winters, and no reported wolf harvest (although unreported wolf harvest continued). Scenario A also produced the lowest percentage of pack areas unoccupied (0% unoccupied by 2045), and lowest percentage of years in which the wolf population dropped below $N_e = 50$ (10% of years, 95% CI = 0, 32%; Fig. 3). Despite less frequent severe winters, Scenario A also resulted in the largest decrease in deer population (-36%, 95% CI = -51, -22) and deer hunting opportunity (-60%, 95% CI = -78, -43) among the scenarios, because wolf numbers were high while deer carrying capacity continued to diminish due to post-logging forest succession, wolf predation, and deer hunting pressure. In contrast, Scenario E resulted in the largest declines in wolf abundance (-35%, 95% CI = -89, -21), which included increased harvest of old growth forest, no change in road density, a 30% cap on wolf harvest, and a high future frequency of severe winters. Old forest logging paired with road access, severe winters, and a high cap on wolf hunting and trapping resulted in the lowest rates of pack occupancy and the highest percentage of years dropping below $N_e = 50$ (98%, 95% CI = 81, 100). Deer hunting opportunity was the highest across all scenarios (-19%, 95% CI = -37, -14).

Scenario B, which we considered the most likely scenario, resulted in a median increase of 63% in wolf abundance (95% CI = -42, 122), median rate of pack area vacancy of 25% (95% CI = 0, 74), 52% of years with populations below the QE threshold $N_e = 50$ (95% CI = 0, 100; Fig. 3), and a median decline of 11% in deer abundance (95% CI = -25, -2). The resulting predation services included browsing impacts in a median of 10% of pack ranges by 2045 (95% CI = 0, 23), a reduction from starting median values of 19% (95% CI = 9, 30).

Sensitivity analysis

Deer abundance declined in 22 of the 26 sensitivity models because of ongoing changes in post-logging forest succession; however, wolf abundance increased across all of the sensitivity models, except for wolf harvest regulations with a 30% legal cap or no cap, in part because the

starting value for the models was low based on the ADFG empirical estimate of wolf abundance (Fig. S1). Changes in wolf abundance due to changes in harvest regulations ranged from an increase of 200% (95% CI = 148, 266) if there was no legal or illegal wolf harvest, to a decrease of -30% (95% CI = 30, -90) if there was no cap on harvest. The second most influential variable on wolf abundance was the percentage of deer in wolf diets, which increased by 31–52%. These sensitivity results allow us to evaluate the influence of a variable across a reasonable range of values, but does not allow us to compare the absolute influence among variables on a per-unit basis.

Eliminating deer harvest entirely had a positive effect on both wolf and deer abundance compared to 2015 levels, increasing wolf abundance by 75% (95% CI = -38, 145) and deer abundance by 12%, (95% CI = 5, 16; Table S4, Fig. S1). Although an extreme and unrealistic perturbation, these results suggest wolves and humans are competing for deer in some watersheds and in some years. Imposing moderate deer harvest regulations could increase wolf and deer abundance, although hunting restrictions would reduce ecosystem services of hunting (i.e., protein provisioning to humans, cultural and recreational values).

The ecosystem disservices of severe deer browsing (deer at 90% of carrying capacity or more within a wolf pack's home range) were most strongly influenced by wolf harvest regulations and deer hunting (Table S5, Fig. S2). Starting conditions for the simulation, which represent the lowest estimate of wolf abundance on record, showed that 19% of pack ranges (95% CI = 10, 32) were impacted by severe browsing. When wolf harvest was comprised only of illegal harvest or absent entirely, no pack ranges were heavily browsed by 2045. However, if a 30% cap or no cap on wolf harvest were implemented, 16% (95% CI = 3, 29) of pack ranges were heavily browsed. Without any deer hunting, 71% of pack ranges were heavily browsed (95% CI = 39, 90) compared to only 10% (95% CI = 0, 22) if hunting continued.

Ecosystem services provided by deer hunting were most strongly influenced by wolf harvest regulations and the percentage of deer in wolf diets, whereas disservices created by severe deer browsing were most strongly influenced by trapping regulations and deer hunting (Table S5; Fig. S2). When no wolf harvest occurred, deer hunting services declined drastically (-80%, 95% CI = -87, -66), but so did browsing disservices (0% pack ranges browsed, 95% CI = 0, 0;). Conversely, if wolves went extinct, deer hunting services declined moderately (-18% CI = -29, -14) but browsing disservices rose (29% pack ranges browsed, 95% CI = 10, 32). Wolf diets showed similar, expected inverse relationships between services and disservices: when wolves ate 9.5 deer/year, deer browsing disservices were higher (16% pack ranges browsed, 95% CI = 3, 26), and hunting services declined less (-24%, 95% CI = -38, -16). When wolves ate the maximum of 26 deer/year, browsing disservices were almost eliminated (3% of pack ranges browsed, 95% CI = 0, 16), but hunting services declined considerably (-44%, 95% CI = -63, 23).

Discussion

Our model indicated that wolf populations would likely increase from our initial spring 2015 population for the “No New Action” scenario and scenarios A–C. This prediction was broadly supported by recent population estimates using a DNA-based capture-mark-recapture technique ($n = 316$ wolves estimated for fall 2019; Fig. S3), although there is considerable uncertainty around these empirical estimates as well (ADFG 2020). However, recent wolf harvests have been record-breaking ($n = 165$ harvested winter 2019-2020; ADFG 2020a), and all scenarios

except scenario A resulted in predicted negative population growth in a portion of the simulations, indicating some degree of risk of future decline regardless of scenario. Wolf populations fell below the quasi-extinction threshold of $N_e = 50$ in 10% of years under scenario A, in >50% of the years simulated for scenarios No New Action, B and C, and by at least 97% of years in scenarios D and E. While our results suggest the potential for modest population growth under current and proposed conditions, wolf recovery likely will be well below historical levels and the potential for inbreeding and resulting population declines will likely remain. Moreover, about 70% of pack areas would be vacant in scenarios D and E and resulting potential for ecosystem disservices via deer browse impacts to conifer regeneration are probable in some areas. Our pack areas were static entities that in reality can be fluid and, as we stated previously, we likely underestimated the variation in predator-prey dynamics that would actually occur. Therefore, our simulation results are likely optimistic.

Mortality of wolves from legal and illegal harvest had the greatest influence on wolf abundance, (Louchouart et al. 2021, Musto et al. 2021, Nowak et al. 2021, Santiago-Ávila et al. 2020,) and also strongly affected deer services (hunting) and disservices (browsing impacts to conifers). Many studies of wolf population dynamics identify human exploitation as a primary driver of population change (Fuller et al. 2003) and the sensitivity of wolf population in our model to harvest is consistent with those studies. The effect of roads on wolves within our study area is also strongly linked to rates of mortality from harvest (Person et al. 1996, Person 2001, Person and Russell 2008, Person and Logan 2012); however, our simulations show little effect of new road construction on future wolf population because the simulated increase in road density was small relative to the existing road extent. Similarly, the effects of forest succession on wolf and deer numbers did not vary much between scenarios because all scenarios included the successional transition to stem exclusion in large areas of second-growth that were harvested prior to 2015. Likewise, the influence of new clearcuts transitioning to old second-growth during the 30-year period covered by our simulations minimizes that same influence from new clearcuts is limited because productive forest sites take 25-40 years to fully transition to low-nutrition old second growth (Alaback 1982). Overall, the changes in forest conditions and roads that we included are a small fraction of the changes that have already occurred to those components between the initiation of industrial-scale logging in the mid-1950s and 2015.

Number of deer killed/year/wolf also exerted a strong influence on wolf and deer numbers, reducing both as predation rates increased. Person (2001) modeled the predator-prey system on Prince of Wales Island using a simpler version of our model with a higher per capita rate of predation. He estimated mean and variance of predation rate on deer from incidence of occurrence data in scats collected during all seasons (Kohira and Rexstad 1997, Person et al. 1996), whereas we employed a lower rate of per capita predation based on stable isotope analyses (Szepanski et al. 1999). Both methods likely underestimate actual predation rates because diet composition cannot be easily converted to number of prey killed, particularly when predators such as wolves do not always consume entire carcasses. Severe winters can substantially reduce deer numbers (Brinkman et al. 2011) and increase the ratio of wolves to deer, which may result in wolves suppressing deer population to low levels for multiple years (Ballard et al. 2001, Bowyer et al. 2005). Our simulations failed to express that dynamic, likely because we used low rates of predation and initial population size of wolves. In contrast, model simulations by Person (2001) for conditions similar to our scenarios B and C, showed that severe

winter events reduced deer populations below 50% of K in 39% of individual model runs, and that 16% of those remained below that threshold for ≥ 10 years (Person 2001). The direct consequence for wolves of suppressed deer populations is not immediate food stress because other prey, particularly salmon and beaver, can be temporarily substituted (Darimont et al. 2008). Rather, the belief that wolves are competing for fewer deer will motivate hunters and trappers to kill more wolves legally and illegally (Person and Brinkman 2013).

Our focus was constrained mostly to wolves because ESA decisions are species centric. Nonetheless, to sustain a resilient population of wolves, deer and other prey are required in sufficient numbers to also sustain other predators like black bears and satisfy deer hunters. Predation by black bears had little influence on changes in predator-prey dynamics between wolves and deer, but hunter harvest of deer reduced both deer and wolf numbers. If wolves had been listed as threatened, scenario “A” likely best represents the resulting conditions in which wolf harvest is curtailed and a significant percentage of roads closed to vehicular use. However, deer harvest likely would plunge 43-78% to levels well below current harvests (Harper and McCarthy 2015) and result in a strong backlash against protecting wolves from subsistence and recreational deer hunters. This could introduce substantial instability to the wolf-deer-people system. Most scenarios indicate deer harvests will decline by 20-30% from 2015 levels, raising the risk that retaliatory legal and illegal wolf harvest will increase and suppress wolf populations below our predicted levels.

The results of our analyses suggest that radical changes in system dynamics on POW are possible and highlight the challenge of conserving predator-prey systems, as well as the potential for considerable changes to predation services and disservices. We argue that large mammalian predators are inevitably dependent on complex social-ecological communities and must be considered within the context of a system rather than an individual species population. Ultimately, loss of deer habitat will drive the systemic decline of deer over the coming decades. The proximate threat to wolf viability will likely still be risk of unsustainable legal and illegal wolf harvest rather than prey scarcity. The motivation for hunters and trappers to kill wolves will be driven by their perception of deer abundance, which is influenced not only by relative abundance of deer and wolves but also by landscape changes (Brinkman et al 2009). As areas dominated by clearcuts transition to thick, even-aged second growth, deer hunters can no longer see or hunt deer in those landscapes and their perception of competition with wolves and other hunters for deer on dwindling lands suitable for hunting will continue to grow.

As deer carrying capacity and resulting deer abundance declines, deer will also likely continue to cause browsing disservices by reducing or eliminating red and yellow cedar and slowing regeneration rates of conifers in young clearcuts, especially if populations are regulated by nutrition rather than predation. As we demonstrate here, wolves are likely providing a predation service to the forestry industry by reducing browsing damage, but this service is currently overlooked, despite its potential high value. In our analysis of potential wolf extinction effects, browsing impacts to conifer occurred in 30% of pack ranges by 2045; this percentage could be much higher if hunting does not keep pace with the deer population, and areas with poor access or sightability for hunters are especially likely to show such effects in the absence of wolves. For example, if deer hunting is absent from the system, over 70% of pack ranges would be impacted by severe conifer browsing, even with continued wolf predation. Long timber rotations are one of the limiting factors affecting the competitiveness of the Southeast Alaskan

second-growth timber economy, and the potential for 20 years of delayed regeneration or complete loss of commercially-valuable species, as has been documented on wolf-free neighboring Haida Gwaii (where hunters are unable to regulate the deer population in the absence of wolves) could make this marginal industry unfeasible. Given the simplistic and optimistic way that hunting is included in our models, we are likely over-estimating deer harvest and hunters' abilities to reduce deer browsing. For example, we included no sex structure in our models, implying both sexes are hunted equally, whereas in reality availability of male deer limits hunting opportunity; likewise, we included no habitat limitations to hunting, while in reality older successional forest stages are very difficult habitats in which to spot and successfully hunt deer.

Importantly, deer can provide other important ecosystem services (such as wildlife viewing and existence values) and disservices (such as suppression of berry bushes, reduction of bird and invertebrate biodiversity, and reduction of carbon sequestration) that we do not attempt to estimate (Côté et al. 2004, Martin et al. 2020). While explicitly representing these feedbacks is beyond the scope of our analysis, the effects of predator-prey interactions on ecosystem function are important to consider, especially as worldwide interest in carbon sequestration and biodiversity conservation accelerates (Schmitz et al. 2018). For example, moderate browsing may increase soil organic carbon (SOC) storage by increasing soil bulk density through trampling and compaction and increase plant biodiversity by influencing plant competitiveness and assembly rules (Nishizawa et al. 2016). However, heavy browsing may reduce forest net primary productivity (NPP) and carbon (C) sequestration by removing aboveground biomass, delaying seedling recruitment, and degrading soil structure (Harada et al. 2020). Preferential browsing can also reduce litter quality by removing palatable species (e.g., cedar, huckleberries) and inducing plants to invest in antiherbivore defense compounds and structural tissues (Côté et al. 2004), although high egestion rates could bypass the litter decomposition pathway (Bardgett and Wardle, 2003). Reducing the quality of litter entering the soil ecosystem alters microbial functional traits (Shao et al. 2019), increases SOC mineralization, and decelerates soil nutrient and litter cycling (Harrison et al. 2004). If microbial communities attack existing stocks to access nutrients (a phenomenon known as priming; Kuzyakov et al. 2000), conversion of SOC to CO₂ could flip heavily browsed forests from a regional C sink to source.

Wolf predation could help mitigate, or reverse, SOC loss by inducing trophic cascades that release plants from intense browsing pressures (Callahan et al. 2013, Flagel et al. 2016, Kirchhoff and Person 2008, Schmitz et al. 2018). As recovering plants allocate C belowground, they gain access to limiting nutrients (including from decomposing carcasses that are not exported from the forest by hunters; Daufresne 2021). This C belowground allocation can in turn stimulate rhizosphere microbial communities (Bardgett et al. 1998). Resulting increases in forage quality could not only help stabilize deer and wolf populations, but may also promote efficient microbial biomass production (Liang et al. 2017, Wardle et al. 2002). The retention of microbial byproducts on soil minerals is now thought to be a primary driver of SOC formation and persistence (Lehmann et al. 2020) and could be especially important in Coastal Alaska where more than 60% of total forest C is held in mineral pools (Yatskov et al. 2019). Wolf-regulated increases in microbial efficiency could thus reinforce the forest C sink. The effects of browsing pressure on the soil ecosystem is complex and could exert a positive feedback on SOC (Conant and Paustian 2002), by increasing microbial metabolic efficiency and the formation of new SOC,

or a negative feedback, by increasing priming and SOC loss as CO₂. Browsing and predator-prey interactions modulate the balance between litter inputs and heterotrophic respiration, which is difficult to predict but has large consequences for the forest C balance (Pugh et al. 2019). Explicitly incorporating predator-prey dynamics could improve the predictive capacity of ecosystem models and may reveal additional ecosystem services provided by wolves and deer (Schmitz et al. 2018).

In closing, we argue for a new, integrated approach to forest and wildlife management in Southeast Alaska and beyond, in which the “multi-use” mandate of the US Forest Service grows to encompass the wide variety of valuable ecosystem services provided by forests. From providing incredible beauty for tourists and residents, to sequestering carbon, sheltering biodiversity, and providing livelihoods, food, and cultural values to indigenous and rural residents, this multitude of services should be considered and valued in management planning. Clearly, herbivory can strongly affect above- and below-ground carbon stores, and predators can regulate the numbers and behavior of their prey; there should be a corresponding, concerted effort by USFS to quantify and incorporate these dynamics into their research program and management decisions. We also recommend several specific management actions. First, we recommend that state and federal agencies monitor wolf and deer populations as closely as possible and require accurate and timely reporting of wolf and deer harvests. We also suggest that a cautious approach to management of wolf hunting and trapping within the Prince of Wales Island archipelago is necessary, and that explicit inclusion of social science into management planning would be enormously helpful for managing this social-ecological system. In addition, we urge the U.S. Forest Service to implement existing plans to close roads while preserving access to popular deer hunting areas, and to adopt application of methods to maintain and reestablish understory vegetation in both young and old second-growth stands, such as canopy gaps and small clearcuts (Wolf Technical Committee 2017). New harvest of second-growth forest should be configured to maximize a broad range of ecosystem services across the landscape, not only board-feet of merchantable timber. Restoration treatments should be well distributed within hunter accessible watersheds as well as those closed to vehicular use, ensuring that hunters can harvest deer and that conifers can re-generate in deer-suppressed areas. Finally, a collaborative approach that includes consideration of all stakeholders’ values, notably traditional values, offers the best strategy to ensure compliance with harvest regulations, meet needs of all stakeholders, and help maintain the long-term stability of this social-ecological system.

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Figure 1. Relationship among primary model components, based on connections among major environmental drivers of wolf abundance in the coastal temperate rainforest of Southeast Alaska. Equation (Eq.) numbers reference Appendix A.

Figure 2. The study area, located on Prince of Wales and outlying islands in Southeast Alaska; pack areas in the wolf population model are outlined in blue and towns are shown as black circles. Maps display a) road density in km per km² in each pack area, and b) deer winter carrying capacity (K) based on the interagency deer habitat suitability index, which ranges from very high (76-130 deer per mi²), to high (43-75 deer per mi²), moderate (23-42 deer per mi²), low (7.1-22 deer per mi²), and very low (0-7 deer per mi²)

Figure 3. Projected effects of modeled scenarios on a) annual wolf abundance; b) distribution of final wolf abundance in 2045; c) percent of pack areas vacant annually; d) annual deer abundance; and e) percentage of years during which wolf abundance dropped below a range of quasi-extinction thresholds. Dashed horizontal lines in b) and e) indicate the quasi-extinction threshold of $N = 119$ wolves, the abundance needed to ensure an effective population size (N_e) of 50 wolves..

Figure 4. Change from 2014–2045 in a) percent change of wolf (grey) and deer (brown) abundance, and b) ecosystem services and disservices across model scenarios, with 95 % confidence interval bars. Services and disservices include the % change in deer harvested by hunters and the percentage of pack areas exposed to intensive deer browsing on conifers by 2045.

Figure 1.JPEG

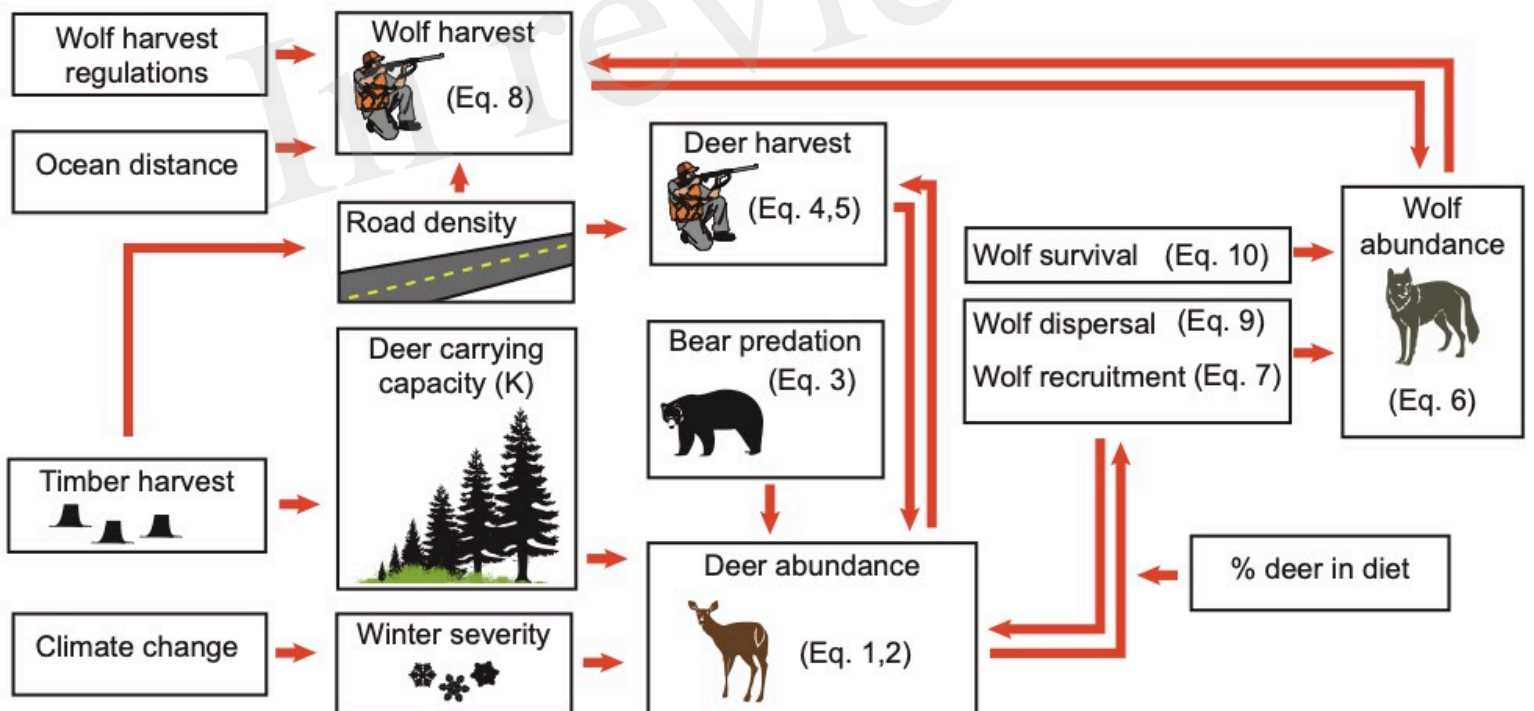


Figure 2.JPEG

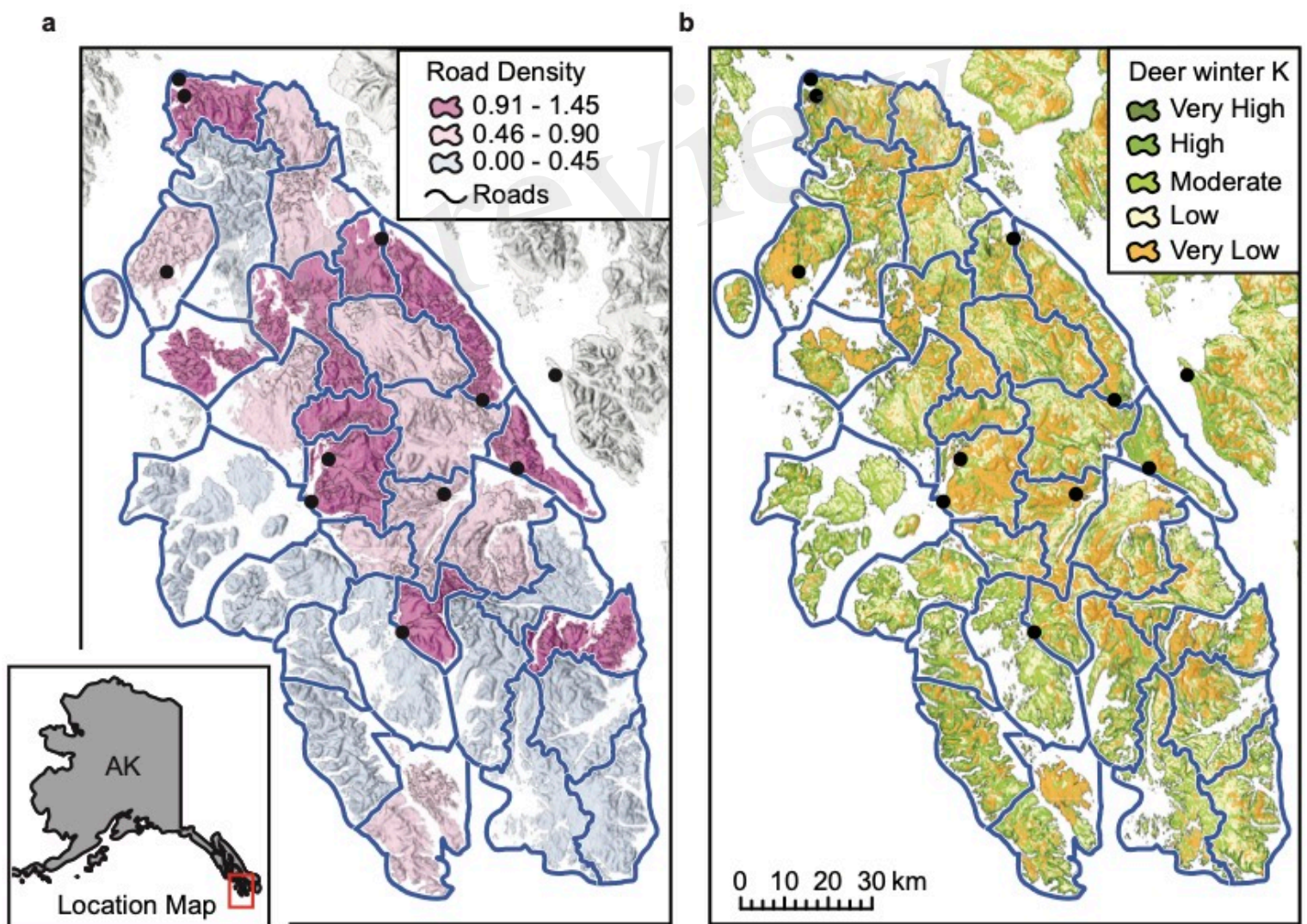


Figure 3.JPEG

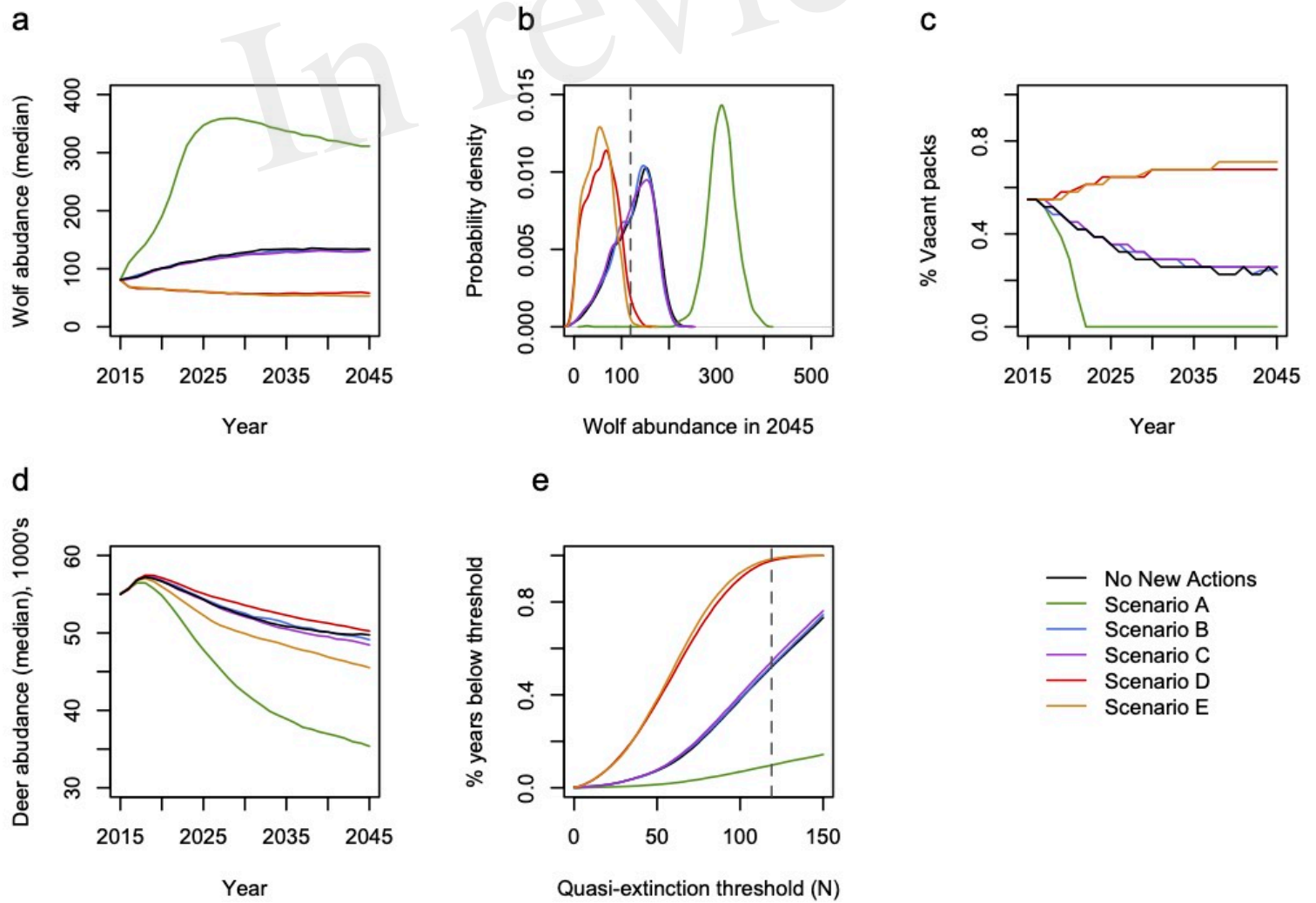


Figure 4.JPEG

